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## THE PROGRESSION OF LIFE IN THE SEA<sup>1</sup>

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THE method we usually follow in the ordinary course of zoological work is to make first, with the unaided eye, a general examination of the animal that interests us, and then study in detail its separate parts with a simple lens, with a low power of the microscope, with gradually increasing powers, until, finally, minute portions are examined with the highest oil-immersion lens. The successful research worker is generally one who, whilst carrying to the utmost limit he can achieve his search into detail, maintains as by instinct a true sense of proportion and holds firmly to the idea of the organism as a whole.

In discussing the living organisms of the sea I shall try to follow a similar plan, thinking of the life of the sea as a whole, built up of individual plants and animals, each in intimate relation with its surroundings, and all interdependent among themselves. But even this is not enough, for we must take still a wider view and keep in mind not only the life of the waters, but that also of the land and of the air, for both, as we shall see, have a bearing on our theme. Deep oceans, coastal waters, shallow seas, rivers and lakes, continents and islands, all play their part in one scheme of organic life—life which had, it seems, one origin, and, notwithstanding migrations and transmigrations from water to land, from land to air, and from land and air back again to the water, remains one closely interrelated whole.

<sup>1</sup> Address of the President of the Section of Zoology of the British Association for the Advancement of Science, Hull, September, 1922.

Both Brandt<sup>2</sup> and Gran<sup>3</sup> have recently emphasized the fact that it is in the coastal waters and shallow seas, which receive much drainage from the land, that plant and animal life are most abundant, the more open oceans far from land being relatively barren; as Schütt puts it, the pure blue of the oceans is the desert color of the seas. This increased production in the coastal waters is due principally to the presence of nitrogen compounds and compounds of phosphorus derived from terrestrial life. From forest, moor and fen, wherever water trickles, the life of the land sends its infinitesimal quota of these essential foodstuffs to fertilize the sea.

When, however, we go back to the beginning of things, we shall probably be right if we say that any influence of terrestrial life upon life in the sea must be left out of account. Different views are still held as to where life in the world had its origin, but no one questions that it began in close connection with water. That it began in the sea, where the necessary elements were present in appropriate concentrations and in an ionized state, is an idea which appeals to many with increasing force the more closely it is examined. This view has been developed recently by Church<sup>4</sup> in his memoir on "The Building of an Autotrophic Flagellate," in which he boldly attempts to trace the progression from the inorganic elements present in sea-water to the unicellular flagellate in the plankton phase, floating freely in the water. The autotrophic flagellate, manufacturing its own food, he regards as the starting-point from which all other organisms, both plants and animals, have sprung. To understand the first step in this progression, the passage from the dead inorganic to the living organic remains, as it has always been, one of the great goals of science, not of biological science alone, but of all science. Recent research has, I think, thrown much light on the fundamental problems involved. In a paper published last year, Baly,

<sup>2</sup> *Wissenschaft. Meeresunters.* Kiel, 18, 1916-20, p. 187.

<sup>3</sup> *Bull. Planktonique.* Cons. Internat., 1912 (1915).

<sup>4</sup> *Biological Memoirs I.* Oxford, 1919.

Heilbron, and Barker,<sup>5</sup> extending and correcting previous work by Benjamin Moore and Webster,<sup>6</sup> have shown that light of very short wave-length ( $\lambda = 200 \mu\mu$ ), obtained from a mercury-vapor lamp, acting upon water and carbon dioxide alone, is capable of producing formaldehyde, with liberation of free oxygen. Light of a somewhat longer wave-length ( $\lambda = 290 \mu\mu$ ) causes the molecules of formaldehyde to unite or polymerize to form simple sugars, six molecules of formaldehyde, for example, uniting to form hexose. The arresting fact brought out in these researches is that the reactions take place, under the influence of light of appropriate wave-lengths, without the help of any catalyst, either organic or inorganic. Where a source of light is used which furnishes rays of many wave-lengths, the simple reaction of the formation of formaldehyde is masked by the immediate condensation of the formaldehyde to sugar, but this formation of sugar can be prevented by adding to the solution a substance which absorbs the longer wave-lengths, so that only the short ones which produce formaldehyde are able to act.

When the formation of sugars is postulated, the introduction of nitrogen into the organic molecule offers little theoretical difficulty; for not only has Moore<sup>7</sup> shown that nitrates are converted into the more chemically active nitrites under the influence of light of short wave-length, but he maintains that marine algae, as well as other green plants, can under the same influence assimilate free nitrogen from the air. Baly<sup>8</sup> also has succeeded in bringing about the union of nitrites with active formaldehyde in ordinary test-tubes by subjecting the mixture to the light of a quartz-mercury lamp.

It will be admitted that these three reactions: (1) the

<sup>5</sup> *Journ. Chem. Soc.*, London, Vols. 119 and 120, 1921, p. 1025. *Nature*, Vol. 109, 1922, p. 344.

<sup>6</sup> *Proc. Roy. Soc. B.*, Vol. 87, p. 163 (1913), p. 556 (1914); Vol. 90, p. 168 (1918).

<sup>7</sup> *Proc. Roy. Soc. B.*, Vol. 90, p. 158 (1918); Vol. 92, p. 51 (1921).

<sup>8</sup> Baly, Heilbron and Hudson, *Journ. Chem. Soc.*, London, Vols. 121 and 122, 1922, p. 1078.

formation of formaldehyde,  $\text{H.CO.H}$ , from carbonic acid,  $\text{OH.CO.OH}$ , with liberation of free oxygen, or, to put it more simply, the direct union of the carbon atom of  $\text{CO}_2$  with a hydrogen atom of  $\text{H}_2\text{O}$ ; (2) the formation of sugars from formaldehyde, and (3) the formation from nitrites and formaldehyde of nitrogenous organic substances, are the most fundamental and characteristic reactions of organic life. It is true that light of such short wave-lengths ( $\lambda = 200 \mu\mu$ ) as were required in Baly's experiments to synthesize formaldehyde does not occur in sunlight as it reaches the earth to-day; but, as we shall see later, the same author has shown that, in the presence of certain substances known as photocatalysts, the reaction can be brought about by ordinary visible light; and from Moore and Webster's work it appears that colloidal hydroxides of uranium and of iron are suitable photocatalysts for the purpose.

If these results of the pure chemist are justified, they go far towards bridging the gap which has separated the inorganic from the organic, and make it not too presumptuous to hazard the old guess that even to-day it is possible that organic matter may be produced in the sea and other natural waters without the intervention of living organisms. We may note here, too, that if we take account of only the most accurate and adequately careful work, the actual experimental evidence at the present time requires the presence of a certain amount of organic matter in the culture medium or environment before the healthy growth of even the simplest vegetable organism can take place. This was illustrated in some experiments made by myself some years ago when attempting to grow a marine diatom, *Thalassiosira gravida*, in artificial sea-water made up from the purest chemicals obtainable dissolved in twice-distilled water. Even after nutritive salts, in the form of nitrates and phosphates, had been added, little or no growth of the diatom occurred. But if as little as 1 per cent. of natural sea-water were added, excellent cultures resulted, in which the growth was as healthy and vigorous as I was able to obtain when natural sea-water was

used entirely as the basis of the culture medium. There was clearly some substance essential to healthy growth contained in the 1 per cent. of natural sea-water, and from further experiments it became practically certain that it was an organic substance. When, for instance, the natural sea-water was evaporated to dryness, the residue slightly heated and redissolved in distilled water, 1 per cent. of this solution added to the artificial culture medium was as potent in producing growth of the diatom as the original natural sea-water had been. When, on the other hand, the residue after evaporation was well roasted at a dull red heat and redissolved in distilled water, the addition of this solution to the artificial culture medium produced no effect and growth did not take place. Growth could also be stimulated by boiling a small fragment of green seaweed (*Ulva*) in the artificial culture medium, the weed being removed before inoculation with the diatom. All this points to the necessity for the presence of some kind of organic matter in the solution before growth can take place. One must not dogmatize, however, for there are many pitfalls in the experimental work and the necessary degree of accuracy is difficult to attain. My own experience of these difficulties culminated when I discovered, covering the bottom of my stock bottle of distilled water—water which had been carefully redistilled from bichromate of potash and sulphuric acid in all-glass apparatus—a healthy growth of mold.

Let us then assume that we are allowed to postulate in primitive sea-water or other natural water organic compounds formed by the energy of light vibrations from ions present in the water, and see how we may proceed to picture the building up of elementary organisms. Without doubt the evolutionary step is a long and elaborate one, for even the simplest living organism is already highly complex both in structure and in function. As the molecules grew more complex by the progressive linkage of the carbon atoms of newly formed carbohydrate and nitrogenous groups, we must suppose that the organic substance, for purely physical reasons, assumed

the colloidal state, and at the same time its surface-tension became somewhat different from that of the surrounding water. With the assumption of the colloidal state, the electric charges on the colloidal particles would produce the effect of adsorption and fresh ions would be attracted from the surrounding medium, producing a kind of growth entirely physical in character. We thus arrive at the conception of a mass of colloidal plasma differing in surface-tension from the water and increasing in size by two processes, the one chemical, due to linkage of carbon atoms; the other physical, brought about by the adsorption of ions by the colloidal particles.

The difference of surface-tension would tend to make the surface a minimum and the shape of the mass spherical. On the other hand, maximum growth would demand maximum exchange with the surrounding medium, and hence maximum surface. From the antagonism of these two factors, surface-tension and growth, there would follow, firstly, the breaking up of the mass into minute particles upon the slightest agitation, and, secondly, changes of form wherever growth involved local alterations of surface-tension, which changes of form would represent the first indication of the property of contractility.

So far we have considered only the process of the building up of the elementary plasmic particles, the anabolic process. Church, whose memoir already referred to I am now closely following, points out that these anabolic operations must from the beginning have been subject to the alternations of day and night, for during the night the supply of external energy is removed. "If during the night," he asks, "the machine runs down, to what extent may it be possible so to delay the onset of molecular finality that some reaction may continue, at a lower rate, until the succeeding day?" And his answer is: "The successful solution of this problem is defined physiologically by the introduction of the conception 'katabolism,' as implying that energy derived from the 'breaking down' of the plasma itself . . . may be regarded as a 'secondary engine,' functional in the absence

of light, and evolved as a last resort in failing plasma." Katabolism persists as the ultimate mechanism in the physiology of animal as contrasted with plant life, but if the suggestion just quoted is sound, it originated, as the first "adaptation" of the organism, to meet the factor of recurring night and day. That the problem was successfully solved we know, but as to the mechanism of its solution we have no key. It is at this point again, to use Church's words, that the "plasma, previously within the connotation of chemical proteid matter, becomes an autotrophic, increasingly self-regulated, and so far individualized entity, to which the term 'life' is applied."

The elementary plasma is thus now fairly launched as an individual living organism, and the great fundamental problems of biology—memory, heredity, variation, adaptation—face us at each step of our further progress. We see in broad outline the conditions the advancing organism had to meet, we see the means by which those conditions were in fact met, we know that only those individuals survived which were able to meet them. Further than this we, the biologists of to-day, have not advanced. The younger generation will pursue the quest, and, with patient effort, much that now lies hidden will grow clear.

The differentiation of the growing particles of plasma into definite layers, which followed, seems natural; first the external layer, in molecular contact with the surrounding water, from which it receives substances from outside in the form of ions, and to which it itself gives off ions; beneath this the autotrophic layer to which light penetrates, and in which, under the influence of the light, new organic substance is built up; in the center a layer to which light no longer penetrates. This central region, the nucleus, depends entirely on the peripheral layers for its own nutrition, and becomes itself concerned only with katabolic processes, those processes of the organism which depend upon the breaking down, and not the building up, of organic substance.

At an early stage in the development of the individual organism the spherical shape, which the organic plasma

was compelled to assume under the influence of surface-tension, underwent an important modification, the effect of which has impressed itself upon all later developments. A spherical organism floating in the water and growing under the direct influence of light would obviously grow more rapidly on the upper side, where the light first strikes it, than it would on the lower side away from the light. There followed, therefore, an elongation of the sphere in the vertical direction, and the definite establishment of an anterior end, the upper end which lay towards the light and at which the most vigorous growth took place. In this way there was established a definite polarity, which has persisted in all higher organisms, a distinction between an anterior and a posterior end. With the concentration of organic substance which took the form of nucleus and reserve food supply, the specific gravity of the plasma would become greater than that of the surrounding water and the organism would tend to sink. The necessity, therefore, arose for some means of keeping it near the surface, that it might continue to grow under the influence of light. The response to this need, however it was attained, came in the development of an anterior flagellum. This we may regard as an elongation in the direction of the light of a contractile portion of the external layer, moving rhythmically, which by its movement counteracted the action of gravity, and acting as a tractor drew the primitive flagellate upwards towards the surface layers, into a position where further growth was possible. That this speculation of Church's represents what was actually accomplished, even though it does not make clear the means by which it was brought about, is shown by the interesting researches of Wager<sup>9</sup> on the rise and fall of the more highly organized flagellate *Euglena*. *Euglena* is a somewhat pear-shaped flagellate, the tapering end being anterior and provided with a single flagellum, which acts as a tractor drawing the organism towards the light. The

<sup>9</sup> *Phil. Trans. Roy. Soc.*, Vol. 201, 1911; and *Science Progress*, Vol. vi, October, 1911, p. 298.

posterior end carries the nucleus and most of the chlorophyll and food reserves. The whole organism has a specific gravity of 1.016, being slightly heavier than the fresh water in which it lives. When dead, or when the flagellum is not moving, it takes up, under the action of gravity alone, a vertical position in the water, with the pointed anterior end uppermost, and the heavier, rounded, posterior end below, and sinks gradually to the bottom.

In a very crowded culture a curious phenomenon is seen, because the organisms tend to aggregate into clusters beneath the surface film, and when they are crowded together in these clusters the flagella cease to work. This makes the whole cluster sink to the bottom under the action of gravity. When the bottom is reached the individuals are spread out by the action of the downward current, and, when they are sufficiently widely apart, the flagella again begin to move, carrying the organisms in a more diffuse stream once more to the surface. The whole culture vessel becomes filled with a series of vertical lines of closely aggregated falling organisms, surrounded by a broad cylinder of disseminated swimming ones, rising to the surface by the action of their flagella. If the conditions are kept uniform, such a circulation of *Euglenas*, falling to the bottom by gravity when the flagella are stopped and returning to the surface under their own power, will continue for days.

The flagellum in this species, therefore, retains its most primitive function of drawing the organism to the light in the surface layer. With the establishment of the flagellum an organ is produced which shows remarkable persistence in both the animal and vegetable kingdoms, and from the existence of the flagellated spermatozoon in the higher vertebrates, in accordance with Haeckel's biogenetic law that the individual in its development repeats or recapitulates the history of the race, we conclude that they also in their earliest history passed through a plankton flagellate phase.

Exactly at what stage in the history of the autotrophic flagellate the first formation of chlorophyll and its allied

pigments took place we have no means of determining, but it may have been before even the flagellum itself had begun. This advance and the subsequent concentration of the pigments into definite chromatophores or chloroplasts doubtless immensely increased the efficiency of the organism in producing the food which was necessary to it. The recent work of Baly and his collaborators becomes here again of the first importance, and though the subject of the part played by chlorophyll in photosynthesis belongs rather to botany and chemistry than to zoology, I may perhaps for the sake of completeness be allowed to refer to it very briefly. I have already said that Baly brought about the synthesis of formaldehyde from  $\text{CO}_2$  and  $\text{H}_2\text{O}$  under the influence of rays of very short wave-length ( $\lambda = 200 \mu\mu$ ) from a mercury-vapor lamp. He was also able to show that when certain colored substances were added to the solution of carbon dioxide in water the same reaction took place under the influence of ordinary visible light. His explanation of this process is that the colored substance known as the photocatalyst absorbs the light rays and then itself radiates, at a lower infra-red frequency corresponding to its own molecular frequency, the energy it has absorbed. At this lower frequency the energy thus radiated is able to activate the carbonic acid, so that the reaction leading to the formation of formaldehyde can and does take place. In the living plant this synthesized formaldehyde probably at once polymerizes to form sugars.

Malachite green and methyl orange, as well as other organic compounds, were found to act as photocatalysts capable of synthesizing formaldehyde, and Moore and Webster's work had previously shown that inorganic substances, such as colloidal uranium oxide and colloidal ferric oxide, can do the same. Chlorophyll in living plants may with some confidence be assumed to operate in a similar way, though no doubt the series of events is more complex, since the green pigment itself is not a single pigment, and others, such as carotin and xanthophyll, are also concerned.

We have tried to picture the gradual building up from elements occurring in sea-water of a chlorophyll-bearing flagellate, capable of manufacturing its own nourishment and able to multiply indefinitely by the simple process of dividing in two. If we assume only one division during each night as a result of the day's work in accumulating food material, such an organism would be able in a comparatively short space of time to occupy all the natural waters of the world. But here we are met by a difficulty which is not easily overcome. Chlorophyll, the photocatalyst, the most essential factor in the building up of the new organic matter, is itself a highly complex organic substance, and in any satisfactory theory its original formation and its constant increase in quantity must be accounted for. Lankester<sup>10</sup> has maintained that chlorophyll must have originated at a somewhat late stage in the development of organic life, and has suggested that earlier organisms may have nourished themselves like animals on organic matter already existing in a non-living state. An alternative hypothesis, which in view of the recent work seems more attractive, is to suppose that the earlier organisms were either activated by some simpler photocatalyst, or that they received the necessary energy at suitable frequency directly from some outside source.

It must not be forgotten, also, that at the time these developments were taking place the conditions of the environment would in many ways have been different from those now existing in the sea. One suggestion of special interest that has been made<sup>11</sup> is that the concentration of carbon dioxide in the atmosphere, and hence also in natural waters, was very much greater than it is to-day. Free oxygen, indeed, may have been entirely absent, and all the free oxygen now present in the air may owe its existence to the subsequent splitting up of carbon dioxide by the action of plant life. With such possibilities of differences in the conditions in this and in so many

<sup>10</sup> "Treatise on Zoology," Part I, Introduction. London, 1909.

<sup>11</sup> See Carl Snyder, "Life without Oxygen," *Science Progress*, Vol. vi, 1912, p. 107.

other directions, may we not be well satisfied if, for the time, we can say that the formation of carbohydrates and proteids has been brought within the category of ordinary chemical operations, which can occur without the previous existence of living substance?

To return once more, however, to the free-swimming, autotrophic flagellate. In the early stages of its history the loss caused by sinking, and so getting below the influence of light and the possibility of further growth, must have been enormous. We may conceive a constant rain of dead and dying organisms falling into the darker regions of the sea, and thus a new field would be offered for the development of any slight advantages which particular individuals might possess. Under such conditions we may suppose that the holozoic or animal mode of nutrition first began in the absorption of one individual by another one, with which it had chanced to come into contact. If the one individual were more vigorous and the other moribund, we should designate the process "feeding," and the additional energy obtained from the food might well cause the individual to survive. If the two individuals which coalesced were both sinking from loss of vigor, the combined energy of the two might make possible a return to the upper water layers, where under the influence of light growth and multiplication would proceed, and we should, I suppose, designate the coalescence "conjugation," or sexual fusion.

Other individuals, again, sinking in shallow water, would stick to solid objects on the sea-floor, whilst the flagellum continued to vibrate. The current produced by the flagellum under these conditions would draw towards the organism dead and disintegrating remains of its fellows, and again we should have ingestion and animal nutrition. At this stage we witness the definite passage from plant to animal life. A further stage is seen when a cup-like depression to receive the incoming particles of food is formed at the base of the flagellum, to be followed still later by a definite mouth.

Any roughening of the external surface of the swim-

ming flagellate, such as we so often find brought about by the deposition of calcareous plates or silicious spicules or the production of ridges or furrows, would tend to slow down its speed of travel, from increased friction with the surrounding water. This would have a similar effect to actual fixation in drawing floating particles by the action of the flagellum, and also lead to animal nutrition. Still another development would occur when the fallen flagellate began to creep along the sea-floor by contractile movements of the plasmic surface, losing its flagellum, and adopting the mode of life of an amœba. That amœba and its allies, the Rhizopods, are descended from a flagellate ancestor is a view suggested by Lankester<sup>12</sup> in 1909, which was adopted by Doflein,<sup>13</sup> and is now strongly advocated by Pascher<sup>14</sup> as a result of much new research.

The transformation from the plant to the animal mode of feeding we can see in action by studying actual organisms which exist to-day. In the course of my work already referred to on the culture of plankton organisms there has on several occasions flourished in the flasks a small flagellate belonging to the group of Chrysomonads, which was first described by Wysotzky under the name of *Pedinella hexacostata*, and to which I drew the attention of Section D at the Cardiff Meeting in 1920. The general form of *Pedinella* resembles that of the common *Vorticella*, but its size is much smaller. The body, which is only about  $5\mu$  in diameter, is shaped like the bowl of a wine glass, and from the base of the bowl, which is the posterior end, a short, stiff stalk extends. From the center of the anterior surface there arises a single long flagellum, surrounded at a little distance by a circle of short, stiff, protoplasmic hairs. Arranged in an equatorial ring just inside the body are six or eight brownish-green chromatophores or chloroplasts. In a healthy cul-

<sup>12</sup> Lankester, "Treatise on Zoology," Part I, London, 1909, p. xxii.

<sup>13</sup> Doflein, "Protozoenkunde," 1916.

<sup>14</sup> Pascher, *Archiv f. Protistenkunde*, Bd. 36, 1916, p. 81, and Bd. 38, 1917, p. 1.

ture *Pedinella* swims about freely by means of a spiral movement of the flagellum, which functions as a tractor, the stalk trailing behind. The chromatophores are large, brightly colored and well developed, and the organism is obviously nourishing itself after the manner of a plant, like any other Chrysomonad. But from time to time a *Pedinella* will suddenly fix itself by the point of the trailing stalk. The immediate effect of this fixing is that a current of water, produced by the still vibrating flagellum, streams towards the anterior surface of the body, and small particles in the water, such as bacteria, become caught up on the anterior surface, the ring of fine stiff hairs surrounding the base of the flagellum being doubtless of great assistance in the capture of this food. One can clearly see bacteria and small fragments of similar size engulfed by the protoplasm of the anterior face of the *Pedinella* and taken into the body. The organism is now feeding as an animal. In some of the cultures in which bacteria were very plentiful nearly all the *Pedinella* remained fixed and fed in the animal way, and when this was so the chromatophores had almost disappeared, though they could still be seen as minute dark dots. We can, as it were, in this one organism see the transition from plant to animal brought about by the simple process of the freely swimming form becoming fixed.

In the group of Dinoflagellates, also—the group to which the naked and armored peridinians belong—the same transition from plant to animal nutrition can be well followed by studying different members of the group. In heavily armored forms, with a rich supply of chromatophores, nutrition is chiefly plant-like or holophytic. In those with fewer chromatophores there is, on the other hand, often distinct evidence of the ingestion of other organisms, and nutrition becomes partly animal-like. Amongst the naked Dinoflagellates such holozoic nutrition is very much developed, and in many species has entirely superseded the earlier method of carbonic acid assimilation.

It is really surprising how many structural features

found in higher groups of animals make their first appearance in these naked Dinoflagellates in conjunction with this change of nutrition, and we seem to be led directly to the metazoa, especially to the Cœlenterata. In *Polykrikos* there are well-developed stinging cells or nematocysts, as elaborately formed as those of *Hydra* or the anemones. In *Pouchetia* and *Erythropsis* well-developed ocelli are found, consisting of a refractive, hyaline, sometimes spherical lens, surrounded by an inner core of red pigment and an outer layer of black; the whole structure is comparable to the ocelli around the bell of a medusa. In *Noctiluca* and in the allied genus *Pavillardia* a mobile tentacle, which is doubtless used for the capture of food, is developed. Division of the nucleus, with the formation of large, distinct chromosomes, has also been described in several of these Dinoflagellates. With the tendency of the cells in certain species to hold together after division and form definite chains, we seem to approach still nearer to the metazoa, until, finally, in *Polykrikos* we reach an organism which may well have given rise to a simple pelagic cœlenterate. It is difficult to resist the suggestion put forward by Kofoid<sup>15</sup> in his recent monograph, that if to *Polykrikos*, with its continuous longitudinal groove which serves it as a mouth, its multicellular and multinucleate body and its nematocysts, we could add the tentacle of *Noctiluca*, and perhaps also the ocellus of *Erythropsis*, "we should have an organism whose structure would appear prophetic of the Cœlenterata and one whose affinities to that phylum and to the Dinoflagellata would be patent." Or it may be that the older view is the correct one here, and that the first cœlenterate came from a spherical colony of simple holozoic flagellates, arranged something on the plan of *Volvox*, in which the posterior cells of the swimming colony, in whose wake food particles would collect, had become more specialized for nutrition than the rest.

Before proceeding, however, to consider the further

<sup>15</sup> Kofoid and Swezy, "The Free-living Unarmored Dinoflagellata." Mem. Univ. California, 1921.

progress of animal life, we must pause for a moment to ask in what direction plant life in the sea developed, from which the increasing animal life derived its nourishment. Here the striking fact is the lack of progress in the free, floating, plankton phase. The plant life of the plankton has never proceeded beyond the unicellular stage, for the plankton diatoms, which with the peridinians form the great, fundamental vegetable food supply of the sea, are only autotrophic flagellates which have lost their flagella, having acquired other means of flotation to keep them in the sunlit region of the upper water layers. Deriving their food, as these plants do, directly from molecules in the sea-water, the factor which is for them of supreme importance is the exposure of maximum surface directly to the water. Hence the minute unicellular form has been the only one to survive as phytoplankton. The marine region in which plant life has succeeded in making some progress is the narrow belt along the shores, where a fixed life is possible, but this belt, limited by the amount of light which penetrates, extends only to a depth of about 15 fathoms. The available area is further restricted to rocky and hard bottoms, and is therefore nowhere great. This is the wave-lashed region of the brown and red seaweeds. In the brown seaweeds a history can still be traced,<sup>16</sup> from the fixture of an autotrophic flagellate to the building up, by laying cell on cell, of the essential structures which afterwards, on transmigration to the land, reached their climax in the forest tree.

But if the flagellate thus rose and gave origin to the flora of the land, it also degenerated, for it adopted a parasitic habit, living in and directly absorbing already formed organic matter. In this way the bacteria arose, whose activities in so many directions influence the life of to-day. This view exceeds in probability, I think, the suggestion often put forward,<sup>17</sup> that it is to the simpler bacteria we must look for the first beginnings of life.

<sup>16</sup> Church, *Botanical Memoirs*, No. 3. Oxford, 1919.

<sup>17</sup> Osborn, "The Origin and Evolution of Life," 1918. Waksman and Joffe, "Micro-organisms concerned in the Oxidation of Sulphur in the

After this digression on the botanical side we must return to the primitive cœlenterate and see on what lines evolution proceeded in the animal world. As a purely plankton organism, swimming freely in the water, the progress of the cœlenterate was not great, and reached, as far as we know, no further than the modern Ctenophore. The Ctenophore seems to represent the culminating point of the primary progression of pelagic animals, which derived directly from the autotrophic flagellate. Further evolution was associated with an abandonment by a cœlenterate-like animal of the pelagic habit, and the establishment of a connection with the sea bottom, either by fixing to it, by burrowing in it, or by creeping or running over it. At a later stage many of the animals which had become adapted to these modes of life developed new powers of swimming, and thus gave rise to the varied pelagic life which we find in the sea to-day; but this must be regarded as secondary, the primary pelagic life, so far as adult animals were concerned, having ended with the evolution of the Ctenophore.<sup>18</sup> Such is the teaching of embryology, the history of the race being conjectured from the development of the individual. In group after group of the animal kingdom, when the details of its embryology become known, the indications are the same—first the active spermatozoon, reminiscent of the plankton flagellate, then the pelagic larval stage, recalling the cœlenterate, and then a bottom-living phase.

The primitive, free-swimming cœlenterate, adopting a fixed habit and becoming attached mouth upwards to solid rock or stone, gave rise to hydroids, anemones and

Soil," *Journal of Bacteriology*, VII, 2, March, 1922. The authors claim that *Thiobacillus thiooxidans* will grow in solutions containing no organic matter. In view of the minute traces of organic matter that suffice for the growth of bacteria and molds, care must be taken, however, in drawing conclusions from experiments made in flasks or tubes closed in the ordinary way with cotton-wool plugs and subsequently sterilized in flowing steam.

<sup>18</sup> There is perhaps a possibility that further knowledge of the embryology of *Sagitta* and its allies might make it necessary to modify this suggestion.

corals, typical inhabitants of the coastal waters, for the sands and muds at greater depths offered few points of attachment sufficiently stable.

A *Volvox*-like colony of simple holozoic flagellates, according to MacBride,<sup>19</sup> commenced to feed upon microscopic organisms lying on the sea bottom, and under these circumstances only the cells of the lower half of the colony would be effective feeders. The upper cells, therefore, lost their flagella and became merely a protective layer, which finally grew downwards outside the others and fixed the colony to the ground. In this way a sponge was formed. The collar cell, so typical of the group, had been developed already by the flagellates, its first inception being perhaps a circle of protoplasmic hairs such as we find in *Pedinella*. But this adoption of a fixed habit, as it were mouth downwards, did not lead very far, and though there has been much elaboration within the group itself, the sponges have remained an isolated phylum, unable to develop into higher forms.

It is in a Ctenophore-like ancestor that we find the line of development to higher animal groups, and this ancestor must have been at one time widely distributed in the seas. Its immediate descendants are familiar to every zoological student in the well-known series of pelagic larval forms. Müller's larva, taking to the bottom, and in its hunt for food gliding over hard surfaces with its cilia, led to the flatworms; the *Pilidium*, developing a thread-like body and creeping into cracks and crevices to transfix its prey, gave rise to the nemertines. A Trochophore, burrowing in soft mud and sand, developed a segmented body which gave it later the power of running on these soft surfaces, and became an annelid worm. Another Trochophore, developing a broad, muscular foot, crept on the sand, and afterwards buried itself beneath it as a lamellibranchiate mollusc, or migrated on to harder surfaces as the gastropod and its allies. *Pluteus*, *Bipinnaria*, *Auricularia*, first fixing, as the crinoids still do, and developing a radial symmetry, afterwards broke free and wandered on the bottom as sea-urchin, star-fish

<sup>19</sup> "Textbooks of Embryology. Invertebrata." London, 1914.

and cucumarian. *Tornaria* developed into *Balanoglossus*, whose structure hints to us that the ascidians and vertebrates came from a similar stock. All the phyla thus represented derive directly from the free-swimming Ctenophore-like ancestor, and only one considerable group, the Arthropods, remains unaccounted for. The evolutionary history of an Arthropod is, however, not in doubt. Its marine representatives, the Trilobites and Crustacea, came directly from annelids, which, after their desertion of a pelagic life to burrow in the sea-floor and run along its surface, again took to swimming, and not only stocked the whole mass of the water with a rich and varied life of Copepods, Cladocera and Schizopods, but gave rise to Amphipods, Isopods, and Decapods, groups equally at home when roaming on the bottom or swimming above it.

Another important addition to the pelagic fauna we should also notice here. From the molluses, creeping on solid surfaces, sprang a group of swimmers, the Cephalopods, which have grown to sizes almost unequaled amongst the animals of the sea.

All these invertebrate phyla had become established and most of them had reached a high degree of development in the seas of Cambrian times. Amongst animals then living there are many which have survived with little change of form until to-day. One is almost tempted to suggest that the life which the sea itself could produce was then reaching its summit and becoming stabilized. Since Cambrian times geologists tell us some thirty million years<sup>20</sup> have passed, a stretch of time which it is really difficult for our imaginations to picture. During that time a change of immense moment has happened to the life of the sea; but if we read the signs aright, that change had its origin rather in an invasion from without than in an evolution from within. Whence came that tribe of fishes which now dominates the fauna of the sea? It would be rash to say that we can give any but a speculative reply to the question, but the probable answer seems to be that fishes were first evolved not to meet

<sup>20</sup> Osborn, "Origin and Evolution of Life," 1918, p. 153.

conditions found in the sea, but to battle with the swift currents of rivers, where fishes almost alone of moving animals can to this day maintain themselves and avoid being swept helplessly away.<sup>21</sup> It was in response to these conditions that elongate, soft-bodied creatures, which had penetrated to the river mouth, developed the slender, stream-lined shape, the rigid yet flexible muscular body, the special provision for the supply of oxygen to the blood to maintain an abundant stock of energy, and all those minute perfections for effective swimming that a fish's body shows. The fact that many sea-fishes still return to the rivers, especially for spawning, supports this view, and it is in accordance with Traquair's classical discoveries of the early fishes of the Scottish Old Red Sandstone, which were for the most part fresh- and brackish-water kinds.

Having developed, under the fierce conditions of the river, their speed and strength as swimmers, the fishes returned to the sea, where their new-found powers enabled them to roam over wide areas in search of food, and gave them such an advantage in attack and defense that they became the predominant inhabitants of all the coastal waters, and as such they remain to-day.

The other great migration of the fishes, also, the migration from the water to the land, giving rise to amphibians, reptiles, birds and mammals, must not be left out of account. The whales, seals and sea-birds, which after developing on land returned again to the waters and became readapted for life in them, are features which can not be neglected.

And so we are brought to the picture of life in the sea as we find it to-day. The primary production of organic substance by the utilization of the energy of sunlight in the bodies of minute unicellular plants, floating freely in the water, remains, as it was in the earliest times, the feature of fundamental importance. The conditions which control this production are now, many of them, known. Those of chief importance are (1) the amount of light which

<sup>21</sup> Chamberlin, quoted in Lull, "Organic Evolution," New York, 1917, p. 462.

enters the water, an amount which varies with the length of the day, the altitude of the sun, and the clearness of the air and of the water; (2) the presence in adequate quantity of mineral food substances, especially nitrates and phosphates; and (3) a temperature favorable to the growth of the species which are present in the water at the time. Experiments with cultures of diatoms have shown clearly that if the food-salts required are present, and the conditions as to light and temperature are satisfactory, other factors, such as the salinity of the water and the proportions of its constituent salts, can be varied within very wide limits without checking growth. The increased abundance of plankton, especially of diatom and peridinian plankton, in coastal waters and in shallow seas largely surrounded by land, such as the North Sea, is due to the supply of nutrient salts washed directly from the land by rain or brought down by rivers. An exceptional abundance of plankton in particular localities, which produces an exceptional abundance of all animal life, is also often found where there is an upwelling of water from the bottom layers of the sea. These conditions are met with where a strong current strikes a submerged bank, or where two currents meet. Food-salts which had accumulated in the depths, where they could not be used owing to lack of light, are brought by the upwelling water to the surface and become available for plant growth. The remarkable richness of fish life in such places as the banks of Newfoundland and the Agulhas Banks off the South African coast, each of which is the meeting-place of two great currents, is to be explained in this way.

Our detailed knowledge of the steps in the food-chain from the diatom and peridinian to the fish is increasing rapidly. The Copepod eats the diatom, but not every Copepod eats every diatom; they make their choice. The young fish eats the Copepod, but again there is selection of kind. Even adult fishes like herring and mackerel, which were formerly supposed to swim with open mouth, straining out of the water whatever came in their way, are now thought largely to select their food.<sup>22</sup>

<sup>22</sup> Bullen, *Journ. Mar. Biol. Assoc.*, 9, 1912, p. 394.

A result of extraordinary interest in connection with the food-chain has recently been brought to light by two sets of investigators working independently. In seeking to explain certain features which he had found in connection with the growth of the cod, Hjort<sup>23</sup> undertook a study of the distribution in marine organisms of the growth stimulant known as vitamin. Fat-soluble vitamin was already known to be present in large quantities in cod-liver oil, and is what probably gives the oil its medicinal value. Hjort was able to trace the vitamin, by means of feeding experiments on rats, in the ripe ovaries of the cod, in shrimps and prawns, which resemble the animals on which the cod feeds, and in diatom plankton and green algae. Jameson, Drummond and Coward<sup>24</sup> cultivated the diatom *Nitzschia closterium*, and by a similar method to that used by Hjort showed that it was extraordinarily potent as a source of fat-soluble vitamin. We thus conclude that this substance, so essential to healthy animal growth, is produced in large quantities by plankton diatoms, and passed on unchanged to the fish through the crustaceans which feed on the diatoms. In the fish the vitamin is first stored in the liver, and with the ripening of the ovary passes into the egg, to be used to stimulate the growth of the next generation. Again we see the fundamental importance of the food-producing activities of the lowest plant life.

Attention has already been drawn to the suggestion that fishes developed their remarkable swimming powers in rivers, in response to a need to overcome the currents, and that they afterwards returned to the sea, where they preyed upon a well-developed and highly complex invertebrate fauna already fully established there. Their speed enabled them to conquer their more sluggish predecessors, whilst they themselves were little open to attack. With the exception of the larger cephalopods, which are of comparatively recent origin, and were probably evolved after the arrival of the fishes, there are few, if any, invertebrates which capture adult fishes as part of their

<sup>23</sup> *Proc. Roy. Soc.*, May 4, 1922.

<sup>24</sup> *Biochemical Journal*, 1922.

normal food. Destructive enemies appeared later in the form of whales and seals and sea-birds, which had developed on the land and in the air.

And now in these last days a new attack is made on the fishes of the sea, for man has entered into the struggle. He came first with a spear in his hand; then, sitting on a rock, he dangled a baited hook, a hook perhaps made from a twig of thorn bush, such as is used to this day in villages on our own east coast. Afterwards, greatly daring, he sat astride a log, with his legs paddled further from the shore, and got more fish. He made nets and surrounded the shoals. Were there time we might trace step by step the evolution of the art of fishing and of the art of seamanship, for the two were bound up together till the day when the trawlers and drifters kept the seas for the battle fleet.

There can be little doubt that in European seas the attack on the fishes in the narrow strip of coastal water where they congregate has become serious. A considerable proportion of the fish population is removed each year, and human activity contributes little or nothing to compensate the loss. We have not, however, to fear the practical extinction of any species of fish, the kind of extinction that has taken place with seals and whales. Fishing is subject to many natural limitations, and when fishing is suspended recovery will be rapid. There is evidence that such recovery took place in the North Sea when fishing was restricted by the War, though the increase which was noted is perhaps not certainly outside the range of natural fluctuations. Until the natural fluctuations in fish population are adequately understood, their limits determined, and the causes which give rise to them discovered, a reliable verdict as to the effect of fishing is difficult to obtain.

If such problems as these are to be solved, the investigation of the sea must proceed on broadly conceived lines, and a comprehensive knowledge must be built up, not only of the natural history of the fishes, but also of the many and varied conditions which influence their lives. The life of the sea must be studied as a whole.

## FAMILY RESEMBLANCES AMONG AMERICAN MEN OF SCIENCE

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THE fascinating problems that concern the causes of individual and group differences among human beings are still with us. Since Galton set out to prove that "a man's natural abilities are derived by inheritance under exactly the same limitations as are the form and physical features of the whole organic world" the biological sciences have made many and notable contributions to the fund of knowledge concerning the derivation "of the form and physical features of the organic world." But the influences by which individual and group differences come about, particularly differences in intellectual performance, seem to have been singularly neglected.

The problem has been avoided partly because of the nature of the material. Human beings are not only complicated in organic construction, but they are mongrel in breed, the period between generations is long and direct experimentation impossible. Few scientific problems are more likely to be disturbed by the bias of the experimenter. The American millionaire or European aristocrat explains differences in the wealth gathering or keeping performance of human beings in terms of innate ability. To the socialist the expression "royal minds" has little basis in fact. Laws, taboos, economic and social conditions are thought to be the proper explanations of differences in human behavior. So deeply do the facts concern the fundamental concepts about the organization of society that debate with its anecdotal method should be supplanted by objective method of the best sort available.

The method of approach used in this study is statistical. The investigation represents an attempt to determine some of the differences or resemblances, the causes

of which have been so often the subject of debate and argument. It is necessary to determine what resemblances or differences exist before causes can be explained. This is a study of family resemblances in intellectual performance, particularly in the field of science.

By limiting the problem to the measurement of resemblances the advice of a gifted and successful worker in this field is followed. He writes:

It is impossible at present to estimate with security the relative shares of original nature, due to sex, race, ancestry and accidental variation, and of the environment, physical and social, in causing the differences found in men. One can only learn the facts, interpret them with as little bias as possible, and try to secure more facts.<sup>1</sup>

By this same limitation it is hoped that a serious and common error will be entirely avoided, namely, the failure to realize the twofold nature of the problem of inheritance as ordinarily discussed. The following analysis is so clear and the need of it so general that it is given at length.

Most sociological writers and some biologists are confused in their use of the concept of heredity. When there is discussion of the relative influence on performance of heredity and environment, by heredity there is sometimes understood the original constitution of the individual and sometimes his resemblance to parents and other relatives. It is conceivable that the original constitution of son and father might be exactly the same and yet the individual be so plastic to environment that under different conditions there would be but slight similarity between their performances. It is also conceivable that there might be no similarity between the original constitution of son and father, and yet the performance of each be determined by his original constitution almost without influence from environment. Under which of these extreme hypotheses would the current sociologist call heredity strong or weak? The word heredity should be reserved for resemblance due to a common germ plasm and some other word found for the constitution of the fertilized ovum or zygote; perhaps the best that can be done is to use this uncouth word. We can then discriminate between the two distinct questions: What is the resemblance between the zygotes of two brothers? How far does the zygote of an individual determine his performance as an adult?<sup>2</sup>

<sup>1</sup> Thorndike, "Educational Psychology," Vol. III, p. 310.

<sup>2</sup> J. McKeen Cattell, "Families of American Men of Science," *Pop. Science Monthly*, May, 1915.

It must not be inferred that this study is an attempt to determine "how far the zygote of an individual determines his performance" or "what is the resemblance between the zygotes of two brothers." It is primarily a statistical measurement of resemblance in performance with particular reference to performance in science. With the results of these measurements at hand, something about the resemblances of the zygotes of near relatives and about how far the zygote of an individual determines his performance may be estimated.

By resemblance is meant, not identity, but degree of similarity. Galton, with the idea of particulate inheritance in mind, early insisted on measuring resemblances as deviations from an average. He justly claims to have been the first to "introduce the law of deviations from the average into the discussions on heredity."<sup>3</sup> Almost forty years later he is found insisting that "probability is the foundation of eugenics."<sup>4</sup> It is here that the statistical method avoids the pitfalls of proof by anecdote. Given a group, selected for some particular sort of performance, the number in any particular degree of relationship showing similar performance may be determined and compared with a similar group of the generality. This is the method used in this study.

The group studied consists of approximately 1,000 American men of science and their families. The wives and the near relatives of the wives of the men of science are included in the data, and the results of the comparisons offer perhaps the most unique contribution of the investigation. The statistical data include only relatives of a degree no more remote than first cousin. These relatives are: brothers and sisters, sons and daughters, fathers and mothers, nieces and nephews, uncles and aunts, grandparents and first cousins.

It may be well here to anticipate a criticism of the use of the term resemblance. Since the group of men of science is made up of persons of known distinction and since

<sup>3</sup> "Hereditary Genius," Preface, 1869.

<sup>4</sup> Spencer lecture, 1907.

resemblance of near relatives is measured in terms of the number of the latter who become distinguished, it is assumed that distinction in any intellectual performance is evidence of resemblance. Thus, a psychologist whose cousin is a psychologist may be said without much fear of contradiction to resemble that relative, but does he really resemble his brother, who is a well-known judge? Does he resemble his distinguished father, a former president of the University of Michigan, a 'gifted administrator'?<sup>5</sup> Apparently, that has been assumed. The fact is, they do resemble each other in so far as they vary in the same direction from the average person in the direction of performance.

The selection of the group of scientific men used has become a classic in individual psychology and need not be related in detail here.<sup>6</sup> Briefly, it may be said, the workers in science were grouped in twelve general divisions as follows: Anatomy, anthropology, botany, chemistry, geology, mathematics, pathology, physics, physiology, psychology and zoology. The workers in each science were arranged in an order of merit by ten leading men in each of those sciences. The average position assigned each man, together with the probable error, was computed. Thus each man's position with the reliability of the figure describing his position was determined, and a thousand of the leading men of science were selected as a group for study. Two selections were made, the first in 1903, the second in 1910. The lists varied somewhat in composition due to deaths, changes of position within the group, removal to a foreign country and the like.<sup>7</sup> The positions attained were not published, that

<sup>5</sup> Since the above was written the psychologist, James Rowland Angell, has become a member of the National Academy of Sciences and the president of Yale University. The question becomes less pertinent but the case more dramatic.

<sup>6</sup> J. McKeen Cattell, "American Men of Science," appendix, second edition, 1910.

<sup>7</sup> A third selection has now been made and will furnish material for a continuation of this study. See "American Men of Science," third edition, J. McKeen Cattell and Dean R. Brimhall, 1921.

information being confidential, but the names of those achieving a position in either selection were marked with an asterisk in the handbook in which they were published. They are referred to in this study as the starred group.

The members of the starred group were asked to report among other data the names of relatives as follows:

Relatives who have done scientific work with designation of relationship and direction of work.

Relatives (with designation of relationship and direction of work) sufficient to warrant inclusion in a book such as "Who's Who," say among the first twenty thousand of a hundred million population.

Relatives (with designation of relationship and direction of work) who have done scientific work or work of distinction in other directions.

Professor Cattell, to whom sole credit is due for gathering the original data, writes concerning requests and replies:

Of one thousand one hundred and fifty-four scientific men from whom information in regard to their families was requested 1,036 replied and 118 did not. Of the replies 16 were blank, sometimes accompanied by the explanation that the information was not readily attainable or the like, 7 were to the effect that the information would be sent later or the like, 13 were received too late, 25 were very imperfect, 975 were usable and in most cases complete. This is an unusually full reply to a questionnaire. For example, in answer to an inquiry in regard to noteworthy relatives addressed to 467 fellows of the Royal Society, Sir Francis Galton received 207 useful replies, and the completely available returns "scarcely exceeded 100."<sup>8</sup>

Following a thorough investigation of that part of the data concerning relatives, in an attempt to supplement and correct them by the use of biographical and genealogical handbooks, the writer sent 186 letters to as many of the men of science, with a report of what had been found in the way of additional information, and asked for corrections and additions. Second and third requests were sometimes sent and in some cases a personal visit to the man of science or near relative was made. As a result the number of usable replies for this study proved to be 956.

<sup>8</sup> "Families of American Men of Science," *Popular Science Monthly*, May, 1915.

Of these 956 records 22 were incomplete in the case of relatives more remote than parents, children, brothers and sisters. Twenty-three were incomplete in kinships more remote than those mentioned. Fully half of the replies of those found to have distinguished relatives were originally incomplete either in names or designation of relationship of names or both. The brother relationship, where it would be supposed complete information would be available, had 84 cases in the original data. This number was raised to nearly 150 through consultation of the handbooks mentioned below. Not more than 25 of those added were found to have first biographical mention at a date later than that of the request for information.

It is unlikely that the ten per cent. who failed to reply did so because of lack of relatives to report; it is unlikely, because that information was a relatively small part of the total requested. Two hundred and fifty-six, or about one fourth of the number replying, were found to have relatives of distinction or relatives who were scientific men; since the other three fourths replied, though they had no relatives to report, it seems reasonable that those who did not reply did not represent a select group. This is further shown to be the case in the number of cross relationships between the two groups. There are found to be brother and cousin relationships that were reported by some of those replying that would have been reported if the others had replied.

The objective criterion used is biographical inclusion in one or more of the three following handbooks: "American Men of Science," "Who's Who in America," "Appleton's Cyclopedie of American Biography." Both editions of "American Men of Science," that is, the editions of 1903 and 1910, were consulted, and biographies found in either were counted. Those found in the original edition of "Appleton's Cyclopedie," published in 1887-88, together with the appendix of 1900 and all ten volumes of "Who's Who in America," covering the pe-

riod from 1910 to 1918, were also included. The first edition of "American Men of Science" contains more than 4,000 men of science, of entire North America, the second edition about 5,500 names. "Appleton's Cyclo-  
pædia of American Biography (1887-88)" contains "above 15,000 prominent native and adopted citizens of the United States, including living persons, from the earliest settlement of the country." In the appendix of 1899-00 "will be found nearly 2,000 notices of Americans who won renown in the war with Spain . . . and of persons of the New World who have become prominent in the peaceful activities of life during the decade," between the appearance of the two publications. The ten volumes of "Who's Who in America" contain 36,915 biographical sketches. The first volume contains 8,602 biographies, while Volume 10 has 22,968. It is evident that the three publications have varying standards of selection, and it becomes necessary to get some statement of the degree of fineness of selection represented by each.

If the reader doubts the validity of any one of the three measures he may disregard those found in that handbook because the lists of names and tables are arranged to that end. That there are biographies of persons included that are out of place is likely and that omissions of others quite deserving occur is also likely, but inclusion represents unusual performance that is a reality.

There is given below the biographical account of one of the persons in the study as it is given in the three different handbooks. Besides adding reality to the data in the lists it will afford a comparison of the characteristic methods employed by the editors of the different publications. The accounts give some idea of the interesting and voluminous records that would be necessary if no more than a brief history of each individual were given. The histories of the men of science and their relatives, if abbreviated in the most careful manner, would make a fair-sized volume. One need only imagine the size of the volume necessary to give an account of the unusual per-

formance of an equal number of people taken at random to see the difference.

BIOGRAPHICAL ACCOUNT OF EDWARD CHARLES PICKERING, AMERICAN  
MEN OF SCIENCE, 1910

Pickering, Prof. Edward C(harles), Harvard College Observatory, Cambridge, Mass. \* *Astronomy, Astrophysics*. Boston, Mass, July 19, 46. B.S. Harvard, 65, A.M. 80, LL.D. 03; California, 86; Michigan, 87; Sc.D. Victoria (England), 00; LL.D. Chicago, 01; Ph.D. Heidelberg, 03; LL.D. Pennsylvania, 06. Instr. math, Lawrence Sci. Sch. Harvard, 65-67; prof. physics, Mass. Inst. Tech, 67-77; *astron. and director, Harvard Col. Observatory*, 77- Bruce Gold Medal, Pacific Astron. Soc; Rumford, Draper, Bruce, two Royal Astron. Soc. and other medals. Nat. Acad; F.A.A. (v. pres, 77); Astron. and Astrophys. Soc. (pres, 06-08); Philos. Soc. (v. pres, 09); fel. Am. Acad; Wash. Acad; hon. mem. N. Y. Acad; cor. mem. Berlin Acad; Soc. astron. de France; Inst. de France; Royal Soc. Upsala; Soc. Lynceorum Nova; St. Petersburgh Imp. Acad; Societies of Cherbourg, Palermo, etc. Stellar photometry and spectroscopy.

ACCOUNT GIVEN IN WHO'S WHO IN AMERICA, VOL. 6, 1910-11

Pickering, Edward Charles, astronomer; *b.* Boston, July 19, 1846. *s.* Edward and Charlotte (Hammond) P; brother of William Henry P. (*q.v.*); *ed.* Boston Latin School; S.B. Lawrence Scientific Sch. (Harvard), 1865 (hon. A.M., 1880; LL.D., univs. of Cal., 1886, Mich., 1887, Chicago, 1901, Harvard, 1903, Pa., 1906; Ph.D., Heidelberg, 1903; D.Sc., Victoria U., Eng., 1900; *m.* Lizzie Wadsworth, *d.* Jared Sparks, Mar. 9, 1874. Instr. mathematics, Lawrence Scientific Sch., 1865-7; Thayer prof. physics, Mass. Inst. Tech., 1867-76; prof. astronomy and dir. Harvard Coll. Obs. since 1876. Established 1st physical lab. in U. S.; under his direction, invested capital and income of the observatory has increased fourfold. Study of light and spectra of the stars have been spl. features of his work; devised meridian photometer and made 1,400,000 measures of the light of the stars with it. By establishing an auxiliary sta. in Arequipa, Peru, Southern stars are also observed, extending the work from pole to pole, in which 200,000 photographs are included. Accompanied Nautical Almanac expdn. to observe total eclipse of sun, Aug. 7, 1869; mem. U. S. Coast Survey expdn. to Xeres, Spain, Dec. 22, 1870. Awarded Henry Draper medal for work on astron. physics; gold medals, Rumford, 1891, Bruce, 1908, Royal Astron. Soc., 1886, 1901. Mem. Nat. Acad. Sciences; hon. mem. of Soc. at Mexico, Cherbourg, Liverpool, Toronto, Upsala and Lund; mem. Royal Astron. Soc., Royal Instn. Acaad. dei Lincei, Royal Prussian, and Royal Irish socs., Royal Soc. of London, Institute de France, Imperial Acad., St. Petersburg; pres. Astron. and Astrophys. Soc.

America, 1906-9; fellow Am. Acad. Arts and Sciences; founder and 1st pres. Appalachian Mountain Club; mem. Century Assn., New York. *Author*: Elements of Physical Manipulation, and 60 volumes of annals and other publications of Harvard Coll. Observatory. *Address*: Harvard Observatory, Cambridge, Mass.

ACCOUNT GIVEN IN APPLETON'S CYCLOPEDIA OF AMERICAN  
BIOGRAPHY, 1887-8

Pickering, Edward Charles, astronomer, b. in Boston, Mass., 19 July, 1846, was graduated in civil engineering course at the Lawrence scientific school of Harvard in 1865. During the following year he was called to the Massachusetts institute of technology as assistant director of physics, of which branch he held the full professorship from 1868 till 1877. Prof. Pickering devised plans for the physical laboratory of the institution, and introduced the experimental method of teaching physics at a time when that mode of instruction had not been adopted elsewhere. His scientific work of these years consisted largely of researches in physics, notably investigations on the polarization of light and the laws of its reflection and dispersion. He also described a new form of spectrum telescope, and invented in 1870 a telephone receiver, which he publicly exhibited. He observed the total eclipse of the sun on 7 Aug., 1869, with the party that was sent out by the Nautical almanac office, at Mt. Pleasant, Iowa, and was a member of the U. S. coast survey expedition to Xeres, Spain, to observe that of 22 Dec., 1870, having, on that occasion, charge of the polariscope. In 1876 he was appointed professor of astronomy and geodesy, and director of the observatory at Harvard, and under his management this observatory has become one of the foremost in the United States. More than twenty assistants now take part in investigations under his direction and the invested funds of the observatory have increased from \$176,000 to \$654,000 during his administration. His principal work since he accepted this appointment has been the determination of the relative brightness of the stars, which is accomplished by the means of a meridian photometer, an instrument specially devised for this purpose, and he has prepared a catalog giving the brightness of over 4,000 stars. Since 1878 he has also made photometer measurements of Jupiter's satellites while they are undergoing eclipse, and of the satellites of Mars and other faint objects. On the death of Henry Draper (q.v.) his widow requested Prof. Pickering to continue important researches on the application of photography to astronomy, as a Henry Draper memorial, and the study of the spectra of the stars has been undertaken on a scale that was never before attempted. A fund of \$250,000, left by Uriah A. Boyden (q.v.) to the observatory, has been utilized for the special study of the advantages of very elevated observing stations. Prof. Pickering has also devoted attention to such objects as mountain surveying, the height and velocity of clouds, papers on which he

has contributed to the Appalachian Club, of which he was president in 1877, and again in 1882. He is an associate of the Royal astronomical society of London, from which in 1886 he received its gold medal for photometric researches, and besides membership in other scientific societies in the United States and Europe he was elected in 1873 to the National academy of sciences, by which body he was further honored in 1887 with the award of the Henry Draper medal for his work on astronomical physics. In 1876 he was elected a vice-president of the American association for the advancement of science, and presented his retiring address before the section of mathematics and physics at the Nashville meeting. In addition to his many papers which number about 100, he prepared "Reports on the Department of Physics," for the Massachusetts institute of technology, and the "Annual Reports of the Director of the Astronomical Observatory," likewise editing the "Annals of the Astronomical Observatory of Harvard College." He has also edited with notes "The Theory of Color in Relation to Art and Art Industry," by Dr. William von Bezold (Boston, 1876), and he is the author of "Elements of Physical Manipulation" (2 parts, Boston, 1873-6).

The raw material of the investigation is found below in the lists of men of science and their relatives. Statistical treatment of these data will follow. They are arranged so that any competent observer can test their validity. While great effort has been made to have the details reliable, it is possible that mistakes may be found in the designation of relationship, but it is thought that such mistakes are few if any.

#### THE MEN OF SCIENCE AND THEIR NEAR RELATIVES OF DISTINCTION

The names of the men of science and their near relatives of distinction are given at the left of the page. The name of the man of science comes first and is followed by a short dash. The names of the relatives follow and are preceded by the letter or letters which tell the relationship. The first name, for example, is Allis, Edward Phelps; he has a cousin (FSiS, a father's sister's son), Callahan, Henry White, whose work is in education. The biography of this relative is found in "Who's Who in America." When the name of a relative is printed in small capitals it shows that the person is known for work

in science. The direction of the performance of the relatives is given at the right of the name. The handbook or books containing his biographical account are shown by the abbreviations at the right. These abbreviations are to be understood as follows: A.M.S, American Men of Science (if preceded by an asterisk the person is in the starred group of men of science); W.W, Who's Who in America; A.C, Appleton's Cyclopedic of American Biography.

Any degree of relationship can be conveniently and accurately described by one, or a combination of two or more, of the following seven letters: S for son, D for daughter, B for brother, Si for sister, F for father, M for mother. Thus, paternal grandfather can be written as FF, meaning father's father, maternal grandfather, MF, meaning mother's father, FBS meaning first cousin or father's brother's son, etc. These symbols precede the name and show the kinship of the person to the man of science.

The men of science are arranged according to the science in which they were recorded as obtaining a place in the starred group. The groups are arranged alphabetically, beginning with the anatomists and closing with the zoologists.

Starred anatomists and near relatives of distinction	Direction of performance	Handbooks containing biographical accounts of relatives
<i>Anatomists</i>		
Allis, Edward Phelps— FSiS Callahan, Henry White	Education	W.W.
Bardeen, Charles Russell— F Bardeen, Charles William	Education	W.W.
Bensley, Robert Russell— B Bensley, Benjamin Arthur	Zoology	A.M.S.
Dwight, Thomas— MB WARREN, JONATHAN MASON MF WARREN, JOHN COLLINS MBS WARREN, JOHN COLLINS	Surgery Surgery Surgery	A.C. A.C. *A.M.S; W.W. A.C.
FBS Dwight, Wilder FBS Dwight, William	Warfare Warfare	A.C. W.W.

Greenman, Milton Jay—			
FBS GREENMAN, JESSE MORE	Botany		*A.M.S; W.W.
Meyer, Arthur William—			
B Meyer, Balthassar Henry	Polit. econ.		W.W.
Spitzka, Edward Anthony—			
F SPITZKA, EDWARD A.	Neurology		A.M.S; A.C.

*Anthropologists*

Dorsey, George Amos—			
B DORSEY, CLARENCE W.	Soil physics		W.W.
B DORSEY, HERBERT GROVE	Physics		A.M.S.
Farrand, Livingston—			
B Farrand, Max	History		W.W.
B Farrand, Wilson	Education		W.W.
Hough, Walter—			
FBS HOUGH, THEODORE	Physiology		*A.M.S; W.W.

*Astronomers*

Doolittle, Charles Leander—			
S Doolittle, Eric	Astronomy		*A.M.S; W.W.
Doolittle, Eric—			
F Doolittle, Charles L.	Astronomy		*A.M.S; W.W.
Frost, Edwin Brant—			
B FROST, GILMAN DUBOIS	Anatomy		A.M.S.
Lowell, Percival—			
B Lowell, Abbott Lawrence	Education		W.W.
Si Lowell, Amy	Poetry		W.W.
MF Lawrence, Abbot	Diplomacy		A.C.
FSID Cabot, Ella Lowell Lyman	Education		W.W.
MSIS Rotch, Abbott Lawrence	Physics		*A.M.S; W.W.
MSIS Rotch, Arthur	Architecture		A.C.
Pickering, Edward Charles—			
B PICKERING, WILLIAM H.	Astronomy		*A.M.S; W.W;
			A.C.
FB PICKERING, CHARLES	Ethnol; Bot.		A.C.
Pickering, William Henry—			
B PICKERING, EDWARD C.	Astronomy		*A.M.S.
FB PICKERING, CHARLES	Ethnol; Bot.		A.C.
Pritchett, Henry Smith—			
F Pritchett, Car Waller	Ministry; Educ.		W.W.

Searle, Arthur—  
B SEARLE, GEORGE MARY Astron; Religion A.M.S; W.W;  
A.C.

Stone, Ormond—  
B Stone, Melville Elijah Journ; Finance W.W; A.C.

Wright, William Hammond—  
M Wright, Johanna Maynard Organization W.W.

*Botanists*

Beal, William James—  
MSiS STEERS, JOSEPH BEAL Zoology A.M.S; W.W.

Bessey, Ernst Athern—  
F BESSEY, CHARLES EDWIN Botany \*A.M.S; W.W.

Bessey, Charles Edwin—  
S BESSEY, ERNST ATHERN Botany \*A.M.S; W.W.

Blakeslee, Albert Francis—  
B Blakeslee, George Hubbard History W.W.  
F Blakeslee, Francis Durbin Ministry W.W.

Bray, William—  
MBS or FSiS FOSTER, LUTHER Botany W.W.

Campbell, Douglas Houghton—  
B CAMPBELL, EDWARD DEM. Chemistry \*A.M.S; W.W.  
B Campbell, Henry Munroe Law W.W.  
F Campbell, James V. Law A.C.

Coker, William Chambers—  
F Coker, James Lide Manufacturing W.W.  
FBS COKER, ROBERT IRWIN Zoology A.M.S; W.W.

Coulter, John Merle—  
B COULTER, STANLEY Botany \*A.M.S; W.W.  
S COULTER, JOHN GAYLORD Botany A.M.S.  
FBS COULTER, SAMUEL MONDS Botany A.M.S.

Coulter, Stanley—  
B COULTER, JOHN MERLE Botany \*A.M.S; W.W;  
A.C.  
BS COULTER, JOHN GAYLORD Botany A.M.S.  
FBS COULTER, SAMUEL MONDS Botany A.M.S.

Coville, Fred Vernon—  
B COVILLE, LUZERNE Medicine A.M.S.

Davis, Bradley Moore—  
FSiS Wood, ROBERT WILLIAMS Physics \*A.M.S; W.W.

Duggar, Benjamin Minge—			
B DUGGAR, JOHN FREDERIC	Agronomy		A.M.S; W.W.
Earle, Franklin Sumner—			
Si HORNE, MARY TRACEY EARLE	Fiction		W.W.
F EARLE, PARKER	Horticulture		A.C.
Fernald, Merritt Lyndon—			
B FERNALD, ROBERT H.	Mech. eng.		A.M.S; W.W.
F FERNALD, MERRITT C.	Edue; Physics; Math.		A.M.S; W.W.
Greenman, Jesse More—			
FBS GREENMAN, MILTON JAY	Anatomy		*A.M.S; W.W.
Halstead, Byron David—			
SiS FAIRCHILD, DAVID G.	Botany		*A.M.S; W.W.
SiS Fairchild, Edwin Milton	Education		W.W.
Kearney, Thomas H.—			
MB Miner, Charles Wright	Warfare		W.W.
Macbride, Thomas Huston—			
FSiS Sterrett, James M.	Ministry; Hist.		W.W.
Pinehot, Gifford—			
B Pinchot, Amos	Law; Politics		W.W.
F Pinchot, James W.	Trade		W.W.
MF Eno, Amos R.	Finance		A.C.
Pound, Rosecoe—			
Si Pound, Louise	Philology		W.W.
Robinson, Benjamin Lincoln—			
B Robinson, James H.	History		W.W.
Shull, George Harrison—			
B SHULL, CHARLES ALBERT	Zoology		A.M.S.
B Scholl, John W.	Literature		W.W.

*Chemists*

Acheson, Edward Goodrich—			
FB Acheson, Marcus Wilson	Law		W.W.
FBS Acheson, Alexander M.	Civil Eng.		W.W.
FBS Acheson, Alexander W.	Med; Polities		W.W.
FBS Acheson, Ernest Francis	Journal; Polities		W.W.
FBS Acheson, Marcus W. Jr.	Law		W.W.
FSiS Brownson, Marcus A.	Ministry		W.W.
FSiD Brownson, Mary Wilson	Literature; Math.		W.W.
Bancroft, Wilder Dwight—			
FF Bancroft, George	History		A.C.

Blair, Andrew Alexander—			
F Blair, Francis Preston	Warfare; Politics	A.C.	
FF Blair, Francis Preston	Journal; Politics	A.C.	
Burgess, Charles Frederick—			
B Burgess, George H.	Railway Eng.	W.W.	
Campbell, Edward DeMille—			
B CAMPBELL, DOUGLAS H.	Botany	*A.M.S; W.W.	
B Campbell, Henry Munroe	Law	W.W.	
F Campbell, James V.	Law	A.C.	
Chatard, Thomas Marean—			
B Chatard, Francis Silas	Educe; Ministry; Med.	W.W; A.C.	
FB Chatard, Frederick	Warfare	A.C.	
Crafts, James Mason—			
MF Mason, Jeremiah	Law	A.C.	
Dabney, Charles William—			
F Dabney, Robert Lewis	Educe; Ministry	A.C.	
Doremus, Charles Avery—			
F DOREMUS, ROBERT O.	Chemistry	A.M.S; W.W; A.C.	
FM Doremus, S. P. (Haines)	Philanthropy	A.C.	
Dunnington, Francis Perry—			
MB Keener, John C.	Ministry	W.W; A.C.	
Franklin, Edward Curtis—			
B FRANKLIN, WILLIAM S.	Physics	*A.M.S; W.W.	
Freer, Paul Casper—			
B Freer, Frederick W.	Art (Painting)	W.W.	
B FREER, OTTO TIGER	Laryngology	W.W.	
Hilgard, Eugene Woldemar—			
B HILGARD, JULIUS	Math; Geodesy	A.C.	
B HILGARD, THEODORE C.	Biology	A.C.	
F HILGARD, THEODORE E.	Law	A.C.	
SiS TITTMAN, OTTO HILGARD	Geodesy	A.M.S; W.W.	
Jackson, Charles Loring—			
FSi Lowell, Anna C. J.	Education	A.C.	
FF Jackson, Patrick Tracy	Manufacturing	A.C.	
MF Loring, Charles Greely	Insurance; Law	W.W; A.C.	
FSiS CABOT, ARTHUR TRACY	Surgery	W.W.	
MBS Loring, William Caleb	Law	W.W.	
FSiS Lowell, C. R.	Warfare	A.C.	
Lewis, Gilbert Newton—			
FB Lewis, Homer Pierce	Education	W.W.	

Lloyd, John Uri—			
B    LLOYD, CURTIS GATES	Botany		A.C.
Loeb, Morris—			
B    Loeb, James	Finance; Archeol.	W.W.	
More, Richard Bishop—			
F    Moore, William Thomas	Ministry; Editing	W.W.	
MF   Bishop, Richard Moore	Politics; Trade	A.C.	
Morely, Edward Williams—			
B    Moreley, John Henry	Ministry; Educ.	W.W.	
Munroe, Charles Edward—			
FBS  Munroe, James Phinney	Mfg; Writing	W.W.	
FBS  Munroe, Kirk	Fiction; Journal	W.W.	
Norris, James Flack—			
B    NORRIS, RICHARD C.	Surgery		W.W.
Norton, Thomas Herbert—			
MB   HORSFORD, EBEN NORTON	Chemistry		A.C.
MF   Horsford, Jeremiah	Warfare		A.C.
MBD  HORSFORD, CORNELIA	Archeology		W.W.
FBS  NORTON, LEWIS MILLS	Chemistry		A.C.
Noyes, William Albert—			
Si   Davidson, Hanna M. N.	Education; Lit.		A.C.
Orndorf, William Ridgely—			
MF   Ridgely, James Lot	Law		A.C.
Osborne, Thomas Burr—			
MB   BLAKE, ELI WHITNEY	Chem; Physics		A.C.
MF   Blake, Eli Whitney	Invention; Mfg.		A.C.
Palmer, Chase—			
FSiS  Harris, George	Ministry; Lit.		W.W.
MBS  Chase, George	Edu; Law		W.W.
Pellew, Charles Ernest—			
F    Pellew, Henry Edward	Philanthropy		W.W.
MB   Jay, John	Diplomacy		A.C.
MF   Jay, William	Law		A.C.
MBS  Jay, William	Law		W.W.
Pond, George Gilbert—			
B    POND, FRANCIS JONES	Chemistry		A.M.S.
Reese, Charles Lee—			
B    Reese, Frederick Focke	Ministry		W.W.
Richards, Theodore William—			
B    RICHARDS, HERBERT M.	Botany		*A.M.S; W.W.
F    Richards, William Trost	Art (Painting)		W.W; A.C.

Sadtler, Samuel Philip—			
F	Sadtler, Benjamin	Ministry	A.C.
MB	Schmucker, B. Melancthon	Ministry	A.C.
MB	Schmucker, Samuel M.	Writing	A.C.
MB	Schmucker, Samuel D.	Law	W.W.
MF	Schmucker, Samuel S.	Educ; Theol.	A.C.
MBS	SCHMUCKER, SAMUEL C.	Botany	A.M.S; W.W.
Sanger, Charles Robert—			
F	Sanger, George P.	Law	A.C.
Saunders, Arthur Percy—			
B	SAUNDERS, CHARLES E.	Chemistry	A.M.S.
B	SAUNDERS, FREDERICK A.	Physics	*A.M.S; W.W.
B	SAUNDERS, WILLIAM E.	Ornith; Bot.	A.M.S.
F	SAUNDERS, WILLIAM	Horticulture	A.M.S.
Sherman, Henry Clapp—			
B	SHERMAN, FRANKLIN, JR.	Entomology	A.M.S.
FBS	Sherman, Frank D.	Architect; Poetry	W.W.
Shimer, Porter William—			
FBS	SHIMER, HERVEY W.	Geology	A.M.S; W.W.
Smith, Edgar Fahs—			
B	SMITH, ALLEN JOHN	Pathology	A.M.S; W.W.
Stieglitz, Julius Oscar—			
B	Stieglitz, Alfred	Photog; Chem.	W.W.
Stillman, John Maxon—			
JB	STILLMAN, STANLEY	Surgery	W.W.
FB	Stillman, Thomas Bliss	Manufacturing	A.C.
FB	Stillman, William James	History; Journal	W.W; A.C.
FBS	STILLMAN, THOMAS B.	Chemistry	*A.M.S; W.W.
Stillman, Thomas Bliss—			
FB	Stillman, Thomas Bliss	Manufacturing	A.C.
FB	Stillman, William James	History; Journal	W.W; A.C.
FBS	STILLMAN, JOHN MAXON	Chemistry	*A.M.S; W.W.
FBS	STILLMAN, STANLEY	Surgery	W.W.
Tuckerman, Alfred—			
B	Tuckerman, Bayard	History	W.W.
MB	Gibbs, Alfred	Warfare	A.C.
MB	Gibbs, George	Antiquarianism	A.C.
MB	GIBBS, OLIVER WOLCOTT	Chemistry	*A.M.S; W.W; A.C.
FF	Tuckerman, Joseph	Ministry	A.C.
MF	GIBBS, GEORGE	Geology	A.C.
FSiS	BECKER, GEORGE F.	Geology	*A.M.S; W.W.
VanSlyke, Lucius Lincoln—			
S	VANSLYKE, DONALD D.	Chemistry	A.M.S.

Venable, Francis Preston—

F	VENABLE, CHARLES S.	Astronomy	W.W.; A.C.
MF	McDowell, James	Politics	A.C.

Waller, Elwyn—

B	Waller, Frank	Architecture	W.W.; A.C.
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*Geologists*

Ashley, George Hall—

B	Ashley, Roseoe Lewis	History; Econ.	W.W.
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Becker, George Ferdinand—

MF	Tuckerman, Joseph	Ministry	A.C.
MBS	TUCKERMAN, ALFRED	Chemistry	*A.M.S; W.W.
MSiS	Tuckerman, Bayard	Biography;	W.W.
		Hist.	

Brooks, Alfred Hulse—

F	BROOKS, THOMAS B.	Geology	A.C.
Si	Paige, Hildegard B.	Fiction	W.W.

Chamberlin, Thomas Corwin—

S	CHAMBERLIN, ROLLIN T.	Geology	A.M.S; W.W.
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Clarke, John Mason—

B	Clarke, Lorenzo Mason	Ministry	W.W.
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Dana, Edward Salisbury—

F	DANA, JAMES DWIGHT	Geology	A.C.
MB	SILLIMAN, BENJAMIN JR.	Chemistry	A.C.
MF	SILLIMAN, BENJAMIN	Chem; Geol.	A.C.

Davis, William Morris—

MF	Mott, James	Ministry	A.C.
MM	Mott, Lucretia	(Quaker)	A.C.

Farrington, Oliver Cummings—

B	Farrington, Wallace R.	Journalism;	W.W.
B	FARRINGTON, EDWARD H.	Hist.	
		Chemistry	W.W.

Gilbert, Grove Karl—

F	Gilbert, Grove Sheldon	Art	A.C.
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Grant, Ulysses Sherman—

F	Grant, Lewis Addison	Law; Warfare	W.W.; A.C.
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Hague, Arnold—

B	HAGUE, JAMES DUNCAN	Geology	A.M.S; W.W;
			A.C.
F	Hague, William	Ministry	A.C.

Harris, Gilbert Dennison—

B	HARRIS, ROLLIN ARTHUR	Geodesy	A.M.S; W.W.
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Hayes, Charles Willard— Si HAYES, ELLEN	Mathematics	A.M.S.
Hitchcock, Charles Henry— F HITCHCOCK, EDWARD	Geol; Educ.	A.C.
B HITCHCOCK, EDWARD	Hygiene	A.M.S; W.W; A.C.
BS HITCHCOCK, EDWARD, JR.	Hygiene	A.M.S; W.W.
Irving, John Duer— F IRVING, ROLAND DUER	Geology	A.C.
Jaggard, Thomas Augustus, Jr.— F Jaggard, Thomas A.	Ministry	W.W; A.C.
Keith, Arthur— MSiS GALE, HOYT STODDARD	Geology	A.M.S.
Mathews, Edward Bennett— B Mathews, Shailer	Educ; Theol.	W.W.
Merriam, John Campbell— B Merriam, Charles E.	Polities; Hist.	W.W.
Merrill, George Perkins— B MERRILL, LUCIUS H.	Chemistry	A.M.S; W.W.
Penrose, Richard Alex. Fullerton— B Penrose, Boies	Polities; Law	W.W.
B PENROSE, CHARLES B.	Surg; Physics	A.M.S; W.W.
B Penrose, Spencer	Eng; Finance	W.W.
F PENROSE, RICHARD A. F.	Surgery	A.M.S; W.W; A.C.
FB Penrose, Clement B.	Law	W.W.
FF Penrose, Charles B.	Law	A.C.
FBS Penrose, Stephen B. L.	Educ; Philos.	W.W.
Pumpelly, Raphael— D Smyth, Margarete P.	Art (Painting)	W.W.
M Pumpelly, Mary Weller	Poetry	A.C.
Rice, William North— S RICE, EDWARD LORANUS	Zoology	*A.M.S; W.W.
Scott, William Berryman— B SCOTT, HUGH LENNOX	Warfare; Anthrop.	W.W.
MB Hodge, Archibald Alex.	Theology	A.C.
MF Hodge, Charles	Theology	A.C.
Smith, James Perrin— B Smith, Charles Forster	Philology	W.W.
Stevenson, John James— MB Willson, James McLeod	Philol; Theol.	A.C.
MF Willson, James Renwick	Philol; Theol.	A.C.
MBS Willson, David Burt	Philol; Theol.	W.W; A.C.

Taylor, Frank Bensley—			
F Stewart, Robert	Politics; Law	W.W.	
Vaughn, Thomas Wayland—			
FBS Vaughn, Horace Worth	Politics; Law	W.W.	
Weed, Walter Harvey—			
F Weed, Samuel Richards	Finance; Lit.	W.W.	
Weller, Stewart—			
MB Marran, J. T.	Law	W.W.	
White, David—			
MSiS Kent, Charles Foster	Hist; Archeol.	W.W.	
Willis, Bailey—			
F Willis, Nathaniel P.	Poetry	A.C.	
FB Willis, Richard Storrs	Music	A.C.	
Winchell, Alexander Newton—			
B WINCHELL, HORACE V.	Geology	A.M.S; W.W.	
F WINCHELL, NEWTON H.	Geol; Archeol.	*A.M.S; W.W;	A.C.
FB WINCHELL, ALEXANDER	Geology	A.C.	
FB Winchell, Samuel R.	Edue;	W.W.	
	Journalism		
Winchell, Newton Horace—			
B WINCHELL, ALEXANDER	Geology	A.C.	
B Winchell, Samuel R.	Edue;	W.W.	
	Journalism		
S WINCHELL, ALEX. N.	Geology	*A.M.S; W.W.	
S WINCHELL, HORACE V.	Geology	A.M.S; W.W.	
FBS Winchell, Benj. La Fon	Ry. Management	W.W.	
FB Winchell, James M.	Ministry	A.C.	
Wright, Frederic Eugene—			
B WRIGHT, CHARLES WILL	Geology	A.M.S.	

#### Mathematicians

Birkoff, George David—			
MB Droppers, Garrett	Polit. Econ.	W.W.	
Coolidge, Julian Lowell—			
B Coolidge, Archibald C.	History	W.W.	
B Coolidge, John Gardiner	Diplomacy	W.W.	
B Coolidge, J. Randolph Jr.	Architecture	W.W.	
FB Coolidge, Jefferson	Diplomacy	W.W; A.C.	
FBS Coolidge, T. Jefferson Jr.	Finance	W.W.	
Fine, Henry Burchard—			
FF Fine, John	Politics; Law	A.C.	

Franklin, Fabian—			
MB Heilprin, Michael	History; Sociol.	A.C.	
MF Heilprin, Phineas M.	Semites	A.C.	
MBS HEILPRIN, ANGELO	Geology	*A.M.S; W.W.; A.C.	
MBS Heilprin, Louis	Philology	W.W; A.C.	
Halsted, George Bruce—			
F Halsted, Oliver Spence	Politics	A.C.	
FF Halsted, Oliver Spence	Philology	A.C.	
Johnson, William Woolsey—			
B Johnson, Charles Fred.	Philology; Math.	W.W.	
McClintock, Emory—			
F McClintock, John	Edu.; Ministry	A.C.	
Moore, Eliakim Hastings—			
F Moore, David Hastings	Edu.; Ministry	W.W.	
Pierce, Charles Santiago Sanders—			
B Peirce, Herbert H. D.	Diplomacy	W.W.	
B PEIRCE, JAMES MILLS	Math; Edu.	*A.M.S; W.W.; A.C.	
F PEIRCE, BENJAMIN	Mathematics	A.C.	
FB PEIRCE, CHARLES HENRY	Chem; Med.	A.C.	
FF Peirce, Benjamin	Library (Harvard)	A.C.	
MF Mills, Elijah Hunt	Polities	A.C.	
Roe, Edward Drake Jr—			
FB Roe, Francis Asbury	Warfare	W.W; A.C.	
Slichter, Charles Summer—			
BS SLICHTER, WALTER I.	Elec. Eng.	A.M.S; W.W.	
Van Vleck, Edward Burr—			
F VAN VLECK, JOHN M.	Astron; Math.	A.M.S; W.W; A.C.	
Veblen, Oswald—			
F VEBLEN, ANDREW A.	Math; Physics	A.M.S; W.W.	
FB Veblen, Thorstein B.	Economics	W.W.	
Wilson, Edwin Bidwell—			
FB Wilson, Frank E.	Polities; Law	W.W.	

*Pathologists*

Biggs, Herman Michael—			
FBS BIGGS, GEORGE PATTEN	Pathology	A.M.S.	
Blumer, George—			
FBS BLUMER, GEORGE ALDER	Neurol; Med.	W.W.	

Cabot, Richard Clarke—			
FBS CABOT, ARTHUR TRACY	Med; Surg.	W.W.	
FBS CABOT, GODFREY L.	Chemistry	W.W.	
Christian, Henry Asbury—			
FBS Christian, George L.	Polities; Lit; War	W.W.	
Cushing, Harvey Williams—			
B CUSHING, HENRY	Geology	A.M.S; W.W.	
B Cushing, William E.	Law	W.W.	
MSiS CREHORE, ALBERT C.	Physics; Eng.	*A.M.S; W.W.	
MSiS CREHORE, WILLIAM W.	Mech. Eng.	W.W.	
Dana, Charles Loomis—			
B Dana, John Cotton	Library	W.W.	
Dock, George—			
Si DOCK, LAVINA L.	Medicine	W.W.	
Ernst, Harold Clarence—			
B Ernest, George Alex.	Law	W.W.	
B ERNST, OSWALD H.	Astron; War; Eng.	W.W.	
MF OTIS, GEORGE ALEX.	Surgery	A.C.	
Flexner, Simon—			
B Flexner, Abraham	Education	W.W.	
Hurd, Henry Mills—			
½B HURD, ARTHUR W.	Psychiatry	W.W.	
Loeb, Leo—			
B LOEB, JACQUES	Zoology	*A.M.S; W.W.	
MacCallum, William George—			
B MACCALLUM, JOHN B.	Anatomy	*A.M.S; W.W.	
F MACCALLUM, GEORGE A.	Ornith; Med.	W.W.	
Mitchell, Silas Weir—			
S MITCHELL, JOHN K.	Neurology	A.M.S; W.W.	
S Mitchell, Langdon E.	Playwriting	W.W.	
F MITCHELL, JOHN K.	Chem; Med.	A.C.	
Musser, John Herr—			
MBS or FSiS Herr, Edwin M.	Elec. Eng.	W.W.	
Park, William Hallock—			
MF Hallock, William S.	Editing; Ministry	A.C.	
MSiS Johnson, William H.	Ministry; Philos.	W.W.	
Putnam, James J.—			
MF Jackson, James	Clin. Med.	A.C.	

Ravenel, Mazyck Porcher—			
FBS RAVENEL, HENRY W.	Botany	A.C.	
MBS PORCHER, FRANCIS P.	Botany; Chem.	A.C.	
Thayer, William Sydney—			
B Thayer, Ezra Ripley	Law	W.W.	
F Thayer, James Bradley	Law	A.C.	
MSiS Simons, Edward	Art (Painting)	W.W.	
Warren, John Collins—			
F WARREN, JONATHAN M.	Surg; Med.	A.C.	
FF WARREN, JOHN COLLINS	Surgery	A.C.	
FSiS DWIGHT, THOMAS	Anatomy	*A.M.S; W.W; A.C.	
Williams, Herbert Upham—			
Si Williams, Eliz. Sprague	Sociology	W.W.	
FSiS Sprague, Carleton	Finance; Art	W.W.	
Welch, William Henry—			
FSiS Cowles, John Guiteau	Finance	W.W.	
MBS Collin, Frederick Welch	Law	W.W.	
MBS Collin, Charles Avery	Law	W.W.	

*Physicists*

Abbe, Cleveland—			
B ABBE, ROBERT	Surg; Physics	A.M.S; W.W.	
S ABBE, CLEVELAND, JR.	Meteorol; Geog.	A.M.S; W.W.	
S ABBE, TRUMAN	Surg; Physiol.	W.W.	
FSiS Smith, Guilford	Finance; Philanth.	W.W.	
Abbot, Charles Greeley—			
FBS Abbot, Henry Larcom	Eng; Warfare	A.M.S; W.W.	
FBS Abbot, Edwin Hale	Finance; Law	W.W.	
Bauer, Louis Agreola—			
B BAUER, WILLIAM C.	Elec. Eng.	A.M.S; W.W.	
Bell, Alexander Graham—			
F BELL, ALEX. MELVILLE	Physiology	A.M.S; W.W; A.C.	
Bell, Louis—			
F Bell, Louis	Warfare; Chem.	A.C.	
FB Bell, James	Politics; Law	A.C.	
FB BELL, JOHN	Editing; Med.	A.C.	
FB BELL, LUTHER V.	Medicine	A.C.	
FB Bell, Samuel Dana	Law	A.C.	
MB Bouton, John Bell	Editing	A.C.	
MF Bouton, Nathaniel	Ministry	A.C.	
FF Bell, Samuel	Politics; Law	A.C.	
FBS Bell, Samuel Newell	Politics; Law	A.C.	

Buckingham, Edgar—			
FF Buckingham, Joseph T.	Editing; Publish.	A.C.	
Crehore, Albert Cushing—			
B CREHORE, WILLIAM W.	Bridge Eng.	W.W.	
MSiS CUSHING, HARVEY W.	Pathology	*A.M.S; W.W.	
MSiS CUSHING, HENRY PLATT	Geology	A.M.S; W.W.	
MSiS Cushing, William E.	Law	W.W.	
Davis, Harvey Nathaniel—			
F DAVIS, NATHANIEL F.	Mathematics	A.M.S; W.W.	
Duane, William—			
B Duane, Russel	Law	W.W.	
FF Duane, William	Publishing	A.C.	
Franklin, William Suddards—			
B FRANKLIN, EDWARD C.	Chemistry	*A.M.S; W.W.	
Hering, Carl—			
B HERING, RUDOLPH	Hydraulic Eng.	A.M.S.	
Humphreys, William Jackson—			
FB Humphreys, Milton W.	Philology	W.W; A.C.	
Ives, Frederick Eugene—			
S IVES, HERBERT EUGENE	Physics	A.M.S.	
Jackson, Dugald Caleb—			
B JACKSON, JOHN PRICE	Elec. Eng.	W.W.	
B Jackson, William B.	Engineering	W.W.	
FSiS Cravath, Paul Drennan	Law	W.W.	
Kent, Norton Adams—			
B Kent, William	Philanthropy	W.W.	
Kimball, Arthur Lalanne—			
B Kimball, A. Redington	Finance	W.W.	
MB Fisher, Samuel Ware	Ministry; Edue.	A.C.	
MBS Fisher, Samuel S., Jr.	Politics; Law	A.C.	
Kinsley, Carl—			
F Kinsley, William W.	Math; Theology	W.W.	
Lyman, Theodore—			
F LYMAN, THEODORE	Zoology	A.C.	
FF Lyman, Theodore	Philanthropy	A.C.	
Magie, William Francis—			
F Magie, William Jay	Politics; Law	W.W.	
Mann, Charles Reborg—			
F Mann, Charles H.	Inventing; Editing; Ministry	W.W.	
FSi Miller, Harriet Mann	Ornith; Writing	W.W.	

Mendenhall, Thomas Corwin— S MENDENHALL, C. E.	Physics	*A.M.S; W.W.
Mendenhall, Charles Elwood— F MENDENHALL, T. C.	Physics	*A.M.S; W.W.; A.C.
More, Lewis Trenchard— B More, Enoch Anson, Jr. B More, Paul Elmer MF Elmer, Lucius Q. C.	Fiction Poetry; Editing Politics; Law	W.W. W.W. A.C.
Northrup, Edwin Fitch— B Northrup, Elliott Judd F Northrup, Ansel Judd FB NORTHRUP, WILLIAM P. MB Fitch, Charles Elliott	Law Law Pathology Editing; Edue.	W.W. W.W.; A.C. A.M.S; W.W. W.W.
Parson, William Barelay— B PARSONS, HARRY DEB.	Mech. Eng.	A.M.S; W.W.
Rotch, Abbott Lawrence— B Rotch, Arthur MF Lawrence, Abbott FBS ROTCH, THOMAS M. MSiS Lowell, Abbott Lawrence MSiS LOWELL, PERCIVAL MSiD Lowell, Amy	Architecture Diplomacy Pediatrics Educ. Astronomy Poetry	A.C. A.C. *A.M.S; W.W. W.W. *A.M.S; W.W.; A.C. W.W.
Saunders, Frederick Albert— B SAUNDERS, ARTHUR P. B SAUNDERS, CHARLES E. B SAUNDERS, WILLIAM E. F SAUNDERS, WILLIAM	Chemistry Chemistry Botany Horticulture	*A.M.S; W.W. A.M.S. A.M.S. A.M.S.
Stevens, Walter LeCont— MB LECONTE, JOHN MB LECONTE, JOSEPH MF LECONTE, LEWIS MBS LECONTE, JOSEPH N.	Physics Geology Botany Mech. Eng.	A.C. W.W.; A.C. A.C. A.M.S; W.W.
Stewart, Oscar Milton— B STEWART, GEORGE W.	Physics	*A.M.S; W.W.
Stewart, George Walter— B STEWART, OSCAR M.	Physics	*A.M.S; W.W.
Trowbridge, Charles Christopher— B Trowbridge, S. B. P. F TROWBRIDGE, W. P.	Architecture Engineering	W.W. A.C.

Very, Frank Washington—

FB	Very, Jones	Lit; Ministry	A.C.
FSi	Very, Lydia Louisa A.	Literature	W.W; A.C.

Wead, Charles Dasson—

MB	Kasson, John Adams	Politics	W.W; A.C.
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Whitman, Frank Perkins—

MSiS	Taylor, James Monroe	Edu; Ethics	W.W; A.C.
MSiD	Bissell, Mary Taylor	Medicine	W.W.

Wood, Robert Williams—

MBS	DAVIS, BRADLEY MOORE	Botany	*A.M.S; W.W.
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Wurts, Alexander Jay—

B	Wurts, John	Law	W.W.
MF	JAY, JOHN CLARKSON	Medicine	A.C.

Zeleny, John—

B	ZELENY, ANTHONY	Physics	*A.M.S; W.W.
B	ZELENY, CHARLES	Zoology	*A.M.S; W.W.

Zeleny, Anthony—

B	ZELENY, CHARLES	Zoology	*A.M.S; W.W.
B	ZELENY, JOHN	Physics	*A.M.S; W.W.

*Physiologists*

Curtis, John Green—

B	Curtis, Edward	Medicine	W.W; A.C.
B	Curtis, Joseph Bridgham	Warfare; Eng.	A.C.
‡B	Curtis, George William	Lit; Publishing	W.W.
BD	Curtis, Constance	Art (Painting)	W.W.
BD	Curtis, Natalie	Music	W.W.

Dawson, Percy Millard—

FB	Dawson, Samuel Edward	Hist; Publishing	A.C.
FSiS	ADAMS, FRANK DAWSON	Geology	A.M.S.

Hare, Hobart Amory—

F	Hare, William Hobart	Ministry	A.C.
FF	Hare, George Enlen	Ministry	A.C.
MF	Howe, Mark A. DeWolfe	Ministry	W.W; A.C.
MBS	Howe, Mark A. DeWolfe	Editing	W.W.

Henderson, Yandell—

MB	YANDELL, DAVID WENDEL	Surgery	A.C.
MF	YANDELL, LUNSFORD	Geology; Med.	A.C.

Hough, Theodore—

FBS	HOUGH, WALTER	Anthropology	*A.M.S; W.W.
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## Lee, Frederic Schiller—

B	LEE, LESLIE ALEXANDER	Zool; Geol.	*A.M.S; W.W.
B	Lee, John Clarence	Edue; Ministry	W.W.
F	Lee, John Stebbins	Edue; Ministry	W.W.

## Lusk, Graham—

F	LUSK, WILLIAM T.	Physiol; Med.	A.C.
MF	Chittenden, Simson B.	Finance; Polities	A.C.

## Sewall, Henry—

FF	SEWELL, THOMAS	Medicine	A.C.
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*Psychologists*

## Angell, James Rowland—

B	Angell, Alexis Caswell	Law	W.W.
F	Angell, James Burrill	Edue; Diplomacy	W.W; A.C.
MF	CASWELL, ALEXIS	Astron; Edue.	A.C.
FBS	ANGELL, FRANK	Psychology	*A.M.S; W.W.

## Angell, Frank—

FB	Angell, James Burrill	Edue; Diplomacy	W.W; A.C.
FBS	Angell, Alexis Caswell	Law	W.W.
FBS	ANGELL, JAMES R.	Psychology	*A.M.S; W.W.

## Bently, Madison—

F	Bently, Charles E.	Ministry	W.W; A.C.
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## Bryan, William Lowe—

B	Bryan, Enoch Albert	Education	W.W.
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## Cattell, James McKeen—

B	CATTELL, HENRY WARE	Pathology	A.M.S; W.W.
F	Cattell, William	Edue; Ministry	A.C.
FB	Cattell, Alexander	Finance; Polities	A.C.
FBS	Cattell, Edward James	Econ; Geog; Lit.	W.W.
FBS	Cattell, William A.	Engineering	W.W.

## Delabarre, Edmund Burke—

B	Delabarre, Frank Alex.	Med; Dentistry	W.W.
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## Dewey, John—

B	Dewey, Davis Rich	Econ; Statistics	W.W.
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## Hall, Granville Stanley—

MBS	BEALS, EDWARD ALDEN	Meteorology	W.W.
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## Jastrow, Joseph—

B	Jastrow, Morris	Theol; Sociol.	W.W.
F	Jastrow, Marcus	Philology	W.W.

## Patrick, George Thomas White—

Si	Patrick, Mary Mills	Edue; Writing	W.W.
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## Sanford, Edmund Clark—

MSiS SHINN, CHARLES H.	Botany	W.W.
MSiD SHINN, MILICENT W.	Psychology	A.M.S; W.W.

## Stratton, George Malcolm—

B	Stratton, Frederick S.	Law	W.W.
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## Strong, Charles Augustus—

F	Strong, Augustus H.	Edue; Theology	W.W; A.C.
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## Thorndike, Edward Lee—

B	Thorndike, Ashley H.	Philology	W.W.
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## Wells, Frederic Lyman—

F	Wells, Benjamin Willis	Language; Econ.	W.W.
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## Woodworth, Robert Sessions—

½B	Woodworth, Frank G.	Edue; Ministry	W.W.
MB	Sessions, William R.	Politics; Agric.	W.W.

*Zoologists*

## Andrews, Ethan Allen—

B	ANDREWS, HORACE	Civil Eng.	A.M.S.
FF	Andrews, Ethan Allen	Lexicography	A.C.

## Bruce, Charles Thomas—

½B	Armstrong, William	Musical Criticism	W.W.
½Si	Benough, Elisa A.	Fiction	W.W.

## Clark, Hubert Lyman—

F	CLARK, WILLIAM S.	Chemistry	A.C.
MF	Richards, William	Education	A.C.
MBS	WILLISTON, ARTHUR L.	Mech. Eng.	W.W.
MBS	Williston, Samuel	Law	W.W.

## Crampton, Henry Edward—

MB	Miller, Charles Henry	Art (Painting)	W.W; A.C.
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## Dahlgren, Ulric—

FB	Dahlgren, Ulric	Warfare	A.C.
FF	DAHLGREN, JOHN A.	Math; Warfare	A.C.

## Dall, William Healey—

F	Dall, Charles Henry A.	Ministry	A.C.
M	Dall, Caroline Wells H.	Lecturing; Lit.	W.W; A.C.

Davenport, Charles Benedict—			
B Davenport, William E.	Sociol; Ministry	W.W.	
Si Davenport, Frances G.	History	W.W.	
Drew, Gilman Arthur—			
B Drew, William Lincoln	Law	W.W.	
Forbes, Stephen Alfred—			
S FORBES, ERNEST B.	Entomology	W.W.	
BS FORBES, ROBERT H.	Soil Chemistry	A.M.S; W.W.	
Gage, Simeon Henry—			
Si GAGE, MARY	Sanitation	W.W.	
Gerould, John Hiram—			
B Gerould, Gordon Hall	Philology	W.W.	
B Gerould, James	Library	W.W.	
Glaser, Otto Charles—			
F GLASER, CHARLES	Chemistry	A.M.S.	
Grave, Caswell—			
B GRAVE, BENJAMIN H.	Zoology	A.M.S.	
Gulick, John Thomas—			
S GULICK, ADDISON	Zoology	A.M.S.	
F Gulick, Peter Johnson	Ministry	A.C.	
BS GULICK, LUTHER H.	Physiol; Educ.	A.M.S; W.W.	
BS Gulick, Sidney Lewis	Ministry; Writing	W.W.	
BD Jewetts, Frances Gulick	Hygiene	W.W.	
FBS Gulick, Charles Burton	Philology	W.W.	
Hargitt, Charles Wesley—			
S HARGITT, GEORGE T.	Geology	A.M.S.	
Herriek, Charles Judson—			
B HERRICK, CLARENCE L.	Neurology	A.M.S.	
Howard, Leland Ossian—			
MSiS Stimson, Henry Lewis	Politics; Warfare	W.W.	
MSiD Keith, Dora Wheeler	Portrait Painting	W.W.	
Jayne, Horace—			
B Jayne, Henry La Barre	Law	W.W.	
F JAYNE, DAVID	Medicine; Pharmacy	A.C.	
Lefevre, George—			
B Lefevre, Albert	Philosophy	W.W.	
B Lefevre, Arthur	Education	W.W.	

Lillie, Frank Rattray—			
B LILLIE, RALPH STAYNER	Zoology		*A.M.S.
Lillie, Ralph Stayner—			
B LILLIE, FRANK R.	Zoology		*A.M.S.; W.W.
Loeb, Jacques—			
B LOEB, LEO	Pathology		*A.M.S.; W.W.
Mayer, Alfred Goldborough—			
F MAYER, ALFRED M.	Physics		A.C.
FB Mayer, Francis B.	Art		A.C.
Merriam, Clinton Hart—			
Si BAILEY, FLORENCE M.	Ornithology		A.M.S.; W.W.
FB Merriam, Augustus C.	Archeol; Philol.		A.C.
Metcalf, Maynard Mayo—			
B Metcalf, Irving Wight	Finance; Ministry		W.W.
B METCALF, WILMOT V.	Chemistry		A.M.S.
FBS Metcalf, Wilder S.	Warfare; Finance		W.W.
Montgomery, Thomas Harrison—			
B Montgomery, James A.	Theol; History		W.W.
MB Morton, James St. Clair	Warfare		A.C.
MB MORTON, THOMAS G.	Surgery		A.C.
MF MORTON, SAMUEL G.	Ethnol; Path; Anat.		A.C.
Moore, John Percy—			
B MOORE, HENRY FRANK	Zoology		A.M.S.; W.W.
Newman, Horatio Hackett—			
F Newman, Albert Henry	History; Theol.		W.W.
Nutting, Charles Cleveland—			
MB Hunt, Henry	Warfare		A.C.
MB Hunt, Lewis Cass	Warfare		A.C.
Osborn, Henry Fairfield—			
B Osborn, William Church	Law; Polities		W.W.
MF Sturges, Jonathan	Trade		A.C.
Peckham, George Williams—			
FB Peckham, R. Wheeler	Law		A.C.
FBS Peckham, R. Wheeler, Jr.	Law		W.W.; A.C.
FBS Peckham, Wheeler H.	Law		W.W.; A.C.
Rice, Edward Loranus—			
F RICE, WILLIAM NORTH	Geology		*A.M.S.; W.W.; A.C.

Shufeldt, Robert Wilson—			
F Shufeldt, Robert W.	Warfare		A.C.
Stone, Witmer—			
F Stone, Frederick D.	History; Library		A.C.
True, Frederick William—			
B TRUE, ALFRED CHARLES	Edue; Agriculture		A.M.S; W.W.
F True, Charles Kitredge	Ministry		A.C.
Verrill, Addison Emery—			
S VERRILL, ALPHEUS H.	Zoology		A.M.S; W.W.
Ward, Henry Baldwin—			
F WARD, RICHARD H.	Bot; Microscopy	A.M.S; W.W;	A.C.
FSi Ward, Anna Lydia	Ethnol; Lexicog.	W.W; A.C.	
Weed, Clarence Moores—			
B WEED, HOWARD EVARTS	Entomology		A.M.S.
Zeleny, Charles—			
B ZELENY, ANTHONY	Physics		*A.M.S; W.W.
B ZELENY, JOHN	Physics		*A.M.S; W.W.

## RELATIVES OF THE WIVES OF MEN OF SCIENCE

The same general plan used in the listing of the men of science and their distinguished relatives is followed below.

*Anatomists*

Donaldson, Mrs. Henry Herbert—			
F Vaux, Calvert	Architecture		A.C.
MB McEntee, Jervis	Architeeture		A.C.

*Anthropologists*

McGee, Mrs. W. J.—			
F NEWCOMB, SIMON	Astronomy		*A.M.S; W.W;
MB Hassler, Ferdinand A.	Med; Literature		A.C.

*Astronomers*

Doolittle, Mrs. Charles Leander—			
B Wolle, Fred	Music		W.W.
S DOOLITTLE, ERIC	Astronomy		*A.M.S; W.W.
F WOLLE, FRANCIS	Botany		A.C.

Frost, Mrs. Edwin Brant—			
F HAZARD, MARSHAL	Editing		W.W.
Holden, Mrs. Edward Singleton—			
B CHAUVENET, REGIS	Mining Eng.		W.W.; A.C.
B CHAUVENET, WILLIAM M.	Chemistry		A.M.S.; W.W.
F CHAUVENET, WILLIAM	Mathematics		A.C.
Loud, Mrs. Frank Herbert—			
B WILEY, WALTER H.	Mining Eng.		W.W.
Mitchell, Mrs. Samuel Alfred—			
F DUMBLE, EDWIN T.	Geology		A.M.S.; W.W.
Pickering, Mrs. Edward Charles—			
F Sparks, Jared	History; Edue.		A.C.
MF Silsbee, Nathaniel	Polities		A.C.
Pritchett, Mrs. Henry Smith—			
FB McAllister, Julian	Warfare		A.C.
FF McAllister, Nath. Hall	Law		A.C.
FBS McAllister, Ward	Jurisprudence		W.W.; A.C.
Wright, Mrs. William Hammond—			
F Leib, Samuel	Law; Horticulture		W.W.

*Botanists*

Atkinson, Mrs. George Francis—			
F KERR, W. C.	Geology		A.C.
Bessey, Mrs. Charles E.—			
S BESSEY, ERNST A.	Botany		*A.M.S.; W.W.
Clements, Mrs. Frederic Edward—			
Si Schwartz, Julia	Literature		W.W.
Coulter, Mrs. John Merle—			
S COULTER, JOHN G.	Botany		A.M.S.
Coulter, Mrs. Stanley—			
B Post, Roswell Oleott	Ministry		W.W.
FB Post, Truman	Ministry		A.C.
Farlow, Mrs. William Gilson—			
Si Horsford, Cornelia	Archeology		W.W.
F HORSFORD, EBEN N.	Chemistry		A.C.
M Horsford, Mary L. H.	Poetry		A.C.
FF Horsford, Jedediah	Warfare; Polities		A.C.
Ganong, Mrs. William Francis—			
B Carman, Bliss	Poetry; Editing		W.W.

Greenman, Mrs. Jesse More—			
MSiS Hartranft, John F.	Politics	A.C.	
Pinchot, Mrs. Gifford—			
F    Bryce, Lloyd S.	Editing; Politics	W.W.	
MF    Cooper, Edward	Finance; Politics	W.W.	
Ramaley, Mrs. Francis—			
F    JACKSON, EDWARD	Ophthalmology	W.W.	
Rose, Mrs. Joseph Nelson—			
FB    Sims, Charles R.	Ministry; Edue.	A.C.	
Stone, Mrs. George Edward—			
F    CLARK, HENRY JAMES	Botany	A.C.	
Wilson, Mrs. William Posell—			
FF    Williams, Charles K.	Politics	A.C.	
<i>Chemists</i>			
Bigelow, Mrs. Samuel Lawrence—			
MF    Harrison, Joseph	Railroad Building	A.C.	
Burgess, Mrs. Charles Frederick—			
B    Jackson, Charles F.	Literature	W.W.	
Cushman, Mrs. Allerton Seward—			
B    Hoppin, Joseph Clark	Archeology; Art	W.W.	
FB    Hoppin, Augustus	Art; Literature	A.C.	
FB    Hoppin, Thomas	Art; Sculptoring	A.C.	
FB    Hoppin, William Jones	Stage; Editing	A.C.	
Franklin, Mrs. Edward Curtis—			
B    Scott, Charles Fred.	Politics	W.W.	
Gies, Mrs. William John—			
MB    Tressler, David	Education	A.C.	
MBS    Tressler, Victor	Education	W.W.	
Kahlenberg, Mrs. Louis—			
B    HEALD, FRED. DEFOREST	Botany	*A.M.S; W.W.	
Long, Mrs. John Harper—			
FB    Stoneman, George	Warfare	A.C.	
Marshall, Mrs. John—			
F    WORMLEY, T. G.	Chemistry	A.C.	

Munroe, Mrs. Charles Edward—			
F BARKER, GEORGE FRED.	Physics	*A.M.S; W.W; A.C.	
Osborne, Mrs. Thomas Burr—			
F JOHNSON, SAMUEL WM.	Chemistry	*A.M.S; W.W; A.C.	
Palmer, Mrs. Chase—			
FBS Edwards, Howard	Edue;	W.W.	
FBD Edwards, Louise	Linguistics	W.W.	
	Literature		
Pellew, Mrs. Charles Ernest—			
F CHANDLER, CHARLES F.	Chemistry	*A.M.S; W.W; A.C.	
FB CHANDLER, WILLIAM H.	Chemistry	A.M.S; W.W; A.C.	
Richards, Mrs. Theodore Wm.—			
F Thayer, Joseph Henry	Theology	W.W; A.C.	
Sanger, Mrs. Charles Robert—			
F Davis, Andrew	Numismatics	W.W; A.C.	
FB Davis, Hasbrook	Warfare	A.C.	
FB Davis, Horace	Manufacturing	A.C.	
FB Davis, John C. B.	Diplomacy	A.C.	
FF Davis, John	Polities	A.C.	
FBS Davis, John	Law; Diplomacy	A.C.	
Saunders, Mrs. Arthur Percy—			
F Brownell, Silas B.	Law	W.W.	
Shimer, Mrs. Porter William—			
B Sandt, George W.	Ministry; Editing	W.W.	
Talbot, Mrs. Henry Paul—			
FSiS Baker, Newton D.	Law; Diplomacy	W.W.	
Tassin, Mrs. Wirt—			
F Moran, Thomas	Art; Exploration	W.W; A.C.	
M Moran, Mary Nimo	Art	A.C.	
FB Moran, Edward	Art	A.C.	
FB Moran, Peter	Art	W.W; A.C.	
FBS Moran, John Leon	Art	W.W; A.C.	
FBS Moran, Edward Percy	Art	W.W; A.C.	
FBD Moran, Annette	Art	W.W.	
Van Slyke, Mrs. Lucius L.—			
S VAN SLYKE, DONALD D.	Chemistry	A.M.S.	

Venable, Mrs. Francis Preston—			
B Manning, James S.	Jurisprudence	W.W.	
FB Manning, Thomas C.	Jurisprudence	A.C.	
Wiechman, Mrs. Ferdinand G.—			
B Damrosch, Frank	Music	W.W.; A.C.	
B Damrosch, Walter	Music	W.W.; A.C.	
F Damrosch, Leopold	Music	A.C.	
Wiley, Mrs. Harvey Washington—			
F Kelton, John C.	Warfare; Sociol.	A.C.	

*Geologists*

Brooks, Mrs. Alfred Hulse—			
F BAKER, FRANK	Anatomy	*A.M.S; W.W.	
Chamberlin, Mrs. T. C.			
S CHAMBERLIN, R. T.	Geology	A.M.S; W.W.	
Cross, Mrs. Whitman—			
FBS Stevens, Isaac I.	Exploration; Eng.	A.C.	
Eastman, Mrs. Charles—			
F CLARK, ALVAN G.	Astronomy	A.C.	
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*(To be continued)*

## AUTOPHORIC TRANSPLANTATION, ITS THEORY AND PRACTISE

PROFESSOR HANS PRZIBRAM

BIOLOGISCHE VERSUCHSANSTALT DER AKADEMIE DER  
WISSENSCHAFTEN, VIENNA

IF a machine breaks down, the mechanical engineer has four ways of repairing it. He may discard the broken parts and reconstruct the whole on a smaller scale; he may fabricate the missing part and fit it into its right place again; he could also take a piece from another machine of more or less similar type, as long as an exchange is made possible by the material of the parts, soldering the broken pieces together or fixing them by screws, wires, etc.; or lastly he may simply exchange the broken part for a whole one, first taking the former out of the broken machine at the points where it was joined, and refitting the new part, taken in like manner out of a similar machine by the same means, in the place of the first. An organism is often just as badly in want of repair as a machine of human fabric. In comparing the two I do not wish to enter here into the controversy of Mechanism *versus* Vitalism. No vitalist will deny that the body of an animal, let us say of vertebrate or arthropod type, is built up of various contrivances the physicist calls machines, and that its functions are best described in physical and chemical terms. It is not the machinery of organized forms that he would throw doubt on, but the mechanical or chemical nature of its driver. Now, when living machinery is broken or maimed, there are the same four possibilities of repair stated above. The organism may shed such parts as are now superfluous for its reduced size and reconstruct itself on the basis of a proportionately diminished form, as in small pieces of planarians, a process called "Morphallaxis," by T. H. Morgan. Secondly, a missing part may be

manufactured anew by the remaining body of the animal, such "Regeneration" not being uncommon even in whole extremities of amphibians and crayfish. But, unfortunately, in the warm-blooded vertebrates this faculty is very limited, not extending much beyond the repair of small pieces of tissue, and never including a whole organ or appendage. It has therefore long been customary in human medicine to try to replace lost parts by "transplantation" of cornea, skin, muscle, bone, or even nerve and blood vessel. Without regard to the composition of the injured part, small pieces or larger portions have been taken from the same or from another individual, and again without special orientation have been grafted upon the wound. All sorts of fastenings have been tried, bandages, plaster, wires, ligatures, but mostly with poor results. The same methods and many others have been applied in experimental zoology, but only when embryonic stages which had not functioned before the operation were used have good results been achieved. Nevertheless it has been demonstrated by A. Carrel that even whole limbs and kidneys may be again healed back in mammals and in the case of the latter again become functionally active. But the tedious method of sewing every sinew, blood vessel and nerve together seems to have prevented till now the general application of this discovery. Carrel's method, as also that of other surgeons, must be compared to the third method of the engineer, when he is soldering or fixing a broken piece on to another, trying to repair the machine without taking it to pieces. Now it is generally simpler to take out the injured piece of a machine, by unscrewing or unsoldering or even by striking it out of the whole by sheer force, so that its connections give way at the points of least resistance, and to replace it by a new one of exactly the same form, than to try and fix the broken parts together again at the point of breakage. Is there a possibility of applying this fourth method of the engineer to the organism? One will, perhaps, at first be inclined to doubt this proposi-

tion. The vitalist will now come forward and claim that the organism is not constituted by parts simply fastened together at certain points, that its unity is the cause of its function; the mechanist will be inclined to doubt the possibility of whole organs regaining their function by "exchange" in animals without high regenerating power, for he has been trained to believe in the destruction of function by the severing of the nerve.

Let us turn to facts. Certain animals, widely distributed through the animal kingdom, practise the faculty of shedding appendages or other parts of their body at certain preformed breaking points. This "autotomy" is also observed in the Crinoid, *Antedon rosaceus*. Working at the Naples Station in 1900 on the regeneration of these Crinoids I wanted to find out if the color in regenerating arms would be influenced by the color of the visceral mass. Now *Antedon* shows a great variety of very distinct shades, such as bright yellow, carmine red and chocolate brown. The visceral mass, easily shed by the animal, was transplanted in proper orientation to a specimen of different color, also void of its viscera. It was immediately accepted by the new owner and clutched tightly to the calyx, as is the usual thing with the normal animal. The connections between the new visceral sac and the body were soon restored, the exchange succeeding in every case. Mouth and anus, both situated on the surface of the visceral sac, became functional again. It is clear that here there is a case of the fourth method of the engineer, namely the replacement of a missing part by a new one of exactly the same form fixed in at the same connecting points as before. One difference is apparent: in the machine there will be little if any activity on the part of the receiver or the new part, whilst in the Crinoid the newly fixed parts are reunited by internal forces. If we want to understand the "exchange" followed by function, it is therefore necessary to know the nature of these forces. Is it possible to account for them on the ground of our present knowledge of living matter? Can we con-

ceive the organism as an engineer mending his own body? When the visceral mass of *Antedon* is not replaced, a new sac is regenerated by the creature. As in all cases of regeneration known to me, it is nothing else than an acceleration of growth going on normally at slower rate, but in the same direction and sense. From this theoretical standpoint, which has been proved to be correct over and over again, we can be satisfied that there are growing forces in the *Antedon* sufficient to ensure the attachment of the new visceral sac.

We have heard that in higher animals regeneration is not as ready to supply lost parts, and as soon as growth ceases, for instance in the imago of insects, the faculty of restoring missing limbs is lost. But a certain degree of repair has been noticed and experimentally tested even here, for instance the closing of holes pricked in the integument of beetles, and even the resprouting of torn-out wings as mere skin duplicatures. In vertebrates a good deal of physiological regeneration is always going on in the tissues, and transplanted pieces of living tissue often become attached in a short time by connective tissue and blood vessels growing over and into them. Will exchange of organs lead under certain conditions to their functional restoration also in such animals as these? The first condition must be the possibility of removing the part to be replaced always in the same place and manner, so as to be sure that it will comprise just the same material and fit in again in the corresponding place of the new host. Planes of preformed breakage would answer best to this condition, but they are generally precluded by the second condition that must be fulfilled, namely retention of the implanted organ by the own forces of the recipient. Such forces may be divided into three groups: first, the natural friction of a mass pressed into a socket, also aided by atmospheric pressure; secondly, the active aid of muscle and nerve clutching the implanted organ and preventing it from falling out of its place; thirdly, the clotting of the body fluids, gluing, as

it were, the graft to the stock. During the last two years my pupils and myself have tried to extend this method, which I now call "autophoric" or self-retaining transplantation, to other cases than the visceral sac of *Antedon*, and we have found that under these conditions function can be restored in a degree unknown till now, at least in developed animals.

The eye of vertebrates may be described as a ball-shaped camera movable by three pairs of levers in all directions of space, connected with its supply of chemicals by the blood vessels and in communication with its operator, the brain, by the optic nerve. If these fixing strings are severed, there is scarcely any attachment to the surroundings save some connecting tissue of unspecialized sort. The "camera" itself will not be injured, if the whole eyeball be taken out of the orbit, and there is scarcely a possibility of altering the points of severance if the enucleation be made quickly and with decision. If the eye is restored to its orbit, it will therefore be possible for all the above-mentioned connections to join again. This was observed as long ago as 1906 by Ruggero Pardo in *Triton*, who made experiments on the necessity of the presence of the optic nerve for the regenerative process in the eye of this amphibian. Unintentionally he had excised the eyeball with the nerve and was much astonished at its reattachment to the orbit. But will eyesight be restored with this reattachment? Pardo was not able to convince himself of this fact, although on histological examination he found the optic nerve regenerated. I have suspected for some time that the vertebrate eye might furnish good material for the restoration of function by autophoric transplantation, as it will in many forms be retained in the orbit by friction and atmospheric pressure alone, aided also in some cases by the eyelids closing over the eyeball, and by its great surface securing wide contact with the blood issuing into the orbit after extirpation. My own first experiments to realize this expectation in new-born rats failed.

In the new-born rat, as in many mammals, the eyes are tightly closed and the lids connected by tissue. This seemed to afford favorable conditions for the exchange of eyes, as they would be kept in place by the tight closure of the eyelids. Having severed the lids, I interchanged the eyes and, as expected, the eyelids shut again tightly and kept the eyeballs in place. But when the eyelids opened again at the normal time, the eyes had grown on, although they were not functional, and totally disappeared in time. Disappointed at this failure, the experiments were discontinued. It is now pretty certain that this poor result was due to the unfavorable conditions obtaining in very young mammals, for we are now able to demonstrate the correctness of my original supposition. Theodor Koppányi, a young Hungarian student, working under my direction in the "Biologische Versuchsanstalt" in Vienna, has succeeded in making the autophoric transplantation of the eye in a variety of species, extending from fish to mammal. The work of Pardo on *Triton* was confirmed, and older rats yielded excellent results. It seems that in the young stages of rats there were difficulties in the way of the eye obtaining a sufficient supply of blood, since also in Koppányi's experiments it was far easier to get the eyes to become reattached and functional in older specimens.

Indeed, it is probable that the pressure of the eyelids exerted on the replaced eyeball in the new-born rats is a hindrance. Grown rats do not close the eyelids tightly upon the eyeballs, so that it is even advisable to pin the lids or sew them together for a day or two, lest the animal whisk out the implanted eyes or scratch at them before they are attached sufficiently firmly to withstand such treatment.

We have been able to show that these replanted eyes are functional, all possible tests yielding positive results and being in striking contrast to those in blinded animals.<sup>1</sup> Microscopical examination of sections through

<sup>1</sup> For details of these experiments I must refer to our previous short

replanted eyes, which had again regained their function, has been made by Professor Walter Kolmer, of the Physiological Institute, University of Vienna, and the re-in-growth of the severed optic nerve-fibers into the optic thalamus is beyond doubt. Professor Kolmer, as all other authorities, to whom the animals with functioning replanted eyes were shown, stated that they would scarcely have believed the fact, without having themselves seen and tested it. Some oculists even refused to believe what they saw, taking refuge in far-fetched explanations for the absolutely normal behavior of the rats and for the connection of retina and brain in anatomical and microscopical preparations. But is the restoration of function in the vertebrate eye really in contradiction to the facts known to us concerning the regeneration in this animal type? If we resort to our theory of regeneration as accelerated growth, moving on the same lines as normal differentiation, and waning with higher specialization, it is necessary to inquire into the normal development of the eye and optic nerve, before answering this question. The vertebrate eye grows from multiple origins, the nervous elements being derived from a fold of the central nervous system (brain). It is generally believed that the nerves of the brain grow in centrifugal direction and are incapable of regeneration, as one does not observe regeneration-cones at the peripheral end of sectioned central nerves as a rule. Ramón y Cajal, on the other hand, thinks that this inability to regenerate is only a consequence of secondary difficulties, regeneration at least commencing when the right nurture is given: this may be accomplished by inserting degenerating nerve-pieces into the pathway of the sectioned nerve. At any rate there would be but little chance of quick and sufficient regeneration, if the eye depended on the nerve growing into it from the brain. Fortunately, as is well known, the fibers of the optic nerve in ontogeny grow communications in the *Akademischer Anzeiger*, Wien; they will be followed by publication in extenso in the *Archiv für Entwicklungsmechanik*, 1922.

centripetally from the retina towards the thalamus opticus. In regeneration this same process need only be repeated. Edward Uhlenhuth, while working at our "Biologische Versuchsanstalt," proved in 1912 that the optic nerve of salamander eyes implanted on the back of the same species grows centripetally towards the spinal cord and even in several instances united with the next spinal ganglion. These transplanted eyes were of course devoid of function, as the nerve had not reached its proper center, but it was of greatest interest to note that the eye, although severed and removed from its natural connection, had totally regenerated after a short period of partial degeneration. Bearing these two points in view, the centripetal growth in ontogeny and the same process in transplanted eyes, we see our theoretical demands for the reattachment of replanted eyes fulfilled: the nerve fibers will grow backwards through the orbit, continuing on their usual path and probably finding good conditions there in the degenerating central stump. The usual assumption that function of a sensitive organ can not be restored after severing the nerve is based on false presumptions, especially the idea that the proper central nerve center is responsible for regeneration. We have in several instances proved that it is not necessary for a body part to be connected with its normal nervous center for regeneration to set in and proceed till completion. I may call attention to Oskar Kurz's transplantations of knees taken from developed tritons and placed on the side of the same animal. Out of this bit of leg all distal parts were regenerated, tibia, fibula, foot and toes, although connection of the nerve-stump remaining in the graft with the normal nervous center in the lumbar region can not have taken place. It is quite another question, how far the presence of nerve is necessary for restoration of normal form; a question often confounded with the inability of reestablishing function after severing of nerves. I will not enter into these problems here, as they are being investigated by several of my fellow-workers

and definite statements can not yet be made. The foundation for the statement that eyes severed from their connection with the brain are not able to regain sight seems to lie in the fact that the optic nerve in mammals, when the eyes are left movable by their proper muscles, can not find its way to a connection with any nerve center, and then degenerates with the other parts of the eye. It seems that the regenerating ends of the optic nerve fibers coming from the retina are carried to and fro by each rolling of the eye and thus fail to connect with the central stump of the nerve. In contrast to this sheering of the fibers in eyes left attached to the orbit after severing of the nerve, the nerve fibers in autophoric replantation reach their goal before the muscles have grown together and become movable again. It must be emphasized that our method involves no injury to the nerve besides a clean cut, and also that Boeke in Amsterdam has been able to obtain results in nerve regeneration far exceeding those of previous experimenters by avoiding suturing or otherwise ill-treating the nerves.

A second opportunity for autophoric replantation is afforded in the vertebrate eye by the lens. It is well known that this part of the eye is derived ontogenetically from an invagination pinching off from the outer layer of ectoderm. The lens of cold-blooded vertebrates, especially urodeles, is capable of regeneration and is easily extracted as a whole, and when it is replanted again into its former place, it fits well into the lens-sac. At my suggestion Berthold Wiesner has applied the method of autophoric replantation to the lens of fish and amphibia; the results show that replanted lenses can clear up again and restore normal eyesight to their bearer. In mammals analogous experiments have not yet succeeded, perhaps because in the rat, the only available mammals for the present, conditions are unfavorable in respect to the relative size of lens, cornea and eyeball. In other forms, as in man, where the lens relative to the size of the eye is much smaller, replantation should succeed, as

the retraction often practised by the oculist is easy, and even regeneration of the lens has been occasionally recorded (see Literature, Przibram, *Regeneration*, 1909).

Unlike the eye of vertebrates, arthropod eyes are not suitable for our method of transplantation. They usually protrude much too far from their socket to be kept in place after their replantation solely by the friction or other forces exerted by the host. A discovery of Walter Finkler has nevertheless put us in position to avail ourselves of the autophoric method for furnishing insects with a new pair of eyes. This young student, having had the opportunity of seeing the results in vertebrates, severed the head of several types of hexapodes from the thorax and, replanting it on its own body or on that of another decapitated individual, observed its retention by the friction and blood clot. There can be no doubt that also in these cases function is restored, all reactions of the normal animal reappearing after a few days or weeks, and the tissues joining quickly. Finkler has worked on the larval, pupal and imaginal state. Perhaps the most astonishing fact is the ready response of the imago to such operations in spite of its lack of regenerative power. But also in this case, as in the higher vertebrates, we shall have to take into account that in our experiments no other processes of reparation are called into play than those of slow physiological regeneration, which still persist in adult organisms. At any rate, in all the tissues of adult insects severed connections are quickly restored, when the organs are left in place, as Finkler could prove. His experiments on autophoric transplantation in insects will be extended to appendages, whilst P. Weiss, Koppányi, Finkler and Wiesner are also occupied with autophoric replantation in parts of the vertebrate body other than the eyes.

#### SUMMARY

1. Well-defined parts of the animal body that may be easily detached at the same connecting points can be replaced by similar new organs under following conditions:

(a) equal size and orientation; (b) simple exchange without exertion of pressure or additional injury to the nerve beyond a clean cut; (c) prevention of loss by the natural means of the animal itself (friction, clasp, blood clot).

2. By this method of "autophoric" or "self-retaining" transplantation, the graft taken from an adult individual and replanted into another may be restored to function, even the nerves of the head reuniting, and the bearer being repaired in every respect.

3. These achievements are in accord with the theory stating regeneration to be nothing else than the acceleration of physiological processes going on all the time in the body of organisms, for it can be demonstrated that the reattachment proceeds in the same sense as the first growth of the nerve. They contradict, however, the general assumption that the maintenance and functional regeneration of organs are dependent on their uninterrupted connection with their special nervous center.

4. Till now we have been able to obtain autophoric replantation with restoration of function in the visceral sac of *Antedon* (Echinoderms—*Przibram*, 1901), in the eyes of fish, amphibia and mammals (Vertebrates—*Koppanyi*, 1921), in the lens of the two former classes (*Wiesner*, 1921), in the heads of insects, walking sticks, water bugs, water beetles (Insects—*Finkler*, 1921) and in other cases not yet ready for publication.

5. Experiments with larval stages of amphibia and insects as compared with the imaginal state of the same species show that there is no radical difference as to the restoration of function after excision and replantation of a part, in mammals (rats) grown-up specimens even seeming to be more favorable for autophoric replantation.

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## SPONTANEOUS METAMORPHOSIS OF THE AMERICAN AXOLOTL

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THE following experiments on axolotl neoteny and metamorphosis are published, not because of the conclusive nature of the results obtained, but the reverse—because of their inconclusiveness. A record of the work seems warranted in order that other investigators of this problem may be spared considerable expense, time and effort due to unsuitability of the material for experimentation.

The latter part of April, 1922, one hundred and nine axolotl larvae of *Ambystoma tigrinum* were received from Albuquerque, New Mexico. These animals were obtained through the courtesy of Mr. J. N. Gladding. They varied in length from four inches to fourteen inches, though the average total length was about seven inches. One animal measured fourteen inches from snout to tail tip, another measured eleven inches. They were the largest individuals of the lot. The animals were in excellent condition on arrival and none showed any indications of metamorphosis.

### EXPERIMENT 1. AUTOPLASTIC THYROID TRANSPLANTATION

May 5, 1922, the thyroids of seven axolotls, seven inches in length, were removed under chlorethane anesthesia and each gland transplanted intraperitoneally into the same individual from which it was taken. The idea was that the acquisition of a new blood and nerve supply by the gland in its new environment might permit the release of the accumulated secretion and so metamorphose the animal. It was shown by the writer ('21) that the thyroid glands of axolotls are highly active metamorphosis-inducing agents providing the hormone escapes into the

blood stream. In these forms there appears to be some inhibition of the secretory (excretory) functions of the thyroid, and the hormone is retained within the gland vesicles.

The experimental animals and their controls were kept in large aquaria with plenty of water and food. One of the grafted animals had metamorphosed by June 27. Three others transformed by July 1; a fifth animal died without transforming July 6. The two remaining axolotls had not metamorphosed by September 1. During the interval between May 21 and September 1, all of the controls spontaneously transformed. The experiment is, of course, without significance because of the unstable nature of the control material. It is highly probable that the operated animals would have metamorphosed just about as rapidly if the thyroid had been left in its normal position.

#### EXPERIMENT 2. HOMOPLASTIC THYROID TRANSPLANTATION

Five seven-inch axolotls were engrafted intraperitoneally with the thyroid gland of other animals of similar size and appropriately controlled by animals transplanted with pieces of muscle tissue.

The transplants were made May 2, 1922. One animal had transformed by June 3, a second by June 6, a third June 11. Two animals remained as larvae and were reengrafted June 11 with axolotl thyroids, and metamorphosed by July 3. In the meantime the controls also transformed. A large series of transplantation experiments were performed, using various endocrine glands, but in every case except two experiments the controls metamorphosed along with the operated individuals.

#### HETEROPLASTIC THYROID TRANSPLANTATION

Four eight-inch axolotls were engrafted intraperitoneally with the glandular tissue of adult *Necturus maculatus*. Each axolotl received the entire thyroid of a single

*Necturus*. The experiment was performed May 15. By June 11 all of the engrafted animals had transformed but none of the controls for this particular group, though normal, untreated animals used as checks for other experiments were metamorphosing during this interval.

Despite the unstable nature of the control material used, this experiment seems fairly sound and indicates that *Necturus* thyroids when injected in sufficient quantity will metamorphose axolotl. To be absolutely reliable this experiment should have been performed upon thyroidectomized forms, but unfortunately the unsuitable nature of the controls was not known until too late.

#### THYROID FEEDING EXPERIMENTS

Five six-inch axolotls were fed desiccated thyroid tissue (Parke, Davis and Company), containing 0.21 per cent. iodine by weight. The feeding was done by means of a pipette May 18. Two animals had transformed by May 27, and all by June 10. None of the controls metamorphosed during this interval but all transformed by July 25. The experiment seems trustworthy, especially in view of similar results obtained by other investigators on animals of the European strain.

#### HETEROPLASTIC PITUITARY TRANSPLANTATION

Five axolotls varying in length from four to seven inches were each grafted with two whole pituitary glands of adult *Rana clamata* frogs. The grafts were made May 5. June 3 one animal metamorphosed; June 7 a second transformed. June 10 the three remaining animals were reengrafted with frog pituitaries. All metamorphosed by June 25.

During the interval between May 5 and June 25 only two of the controls for this particular group transformed, but it must be remembered that control animals of other cultures were metamorphosing. The experiment is recorded for what it is worth, but the writer believes that

injection of fresh pituitary substance does induce axolotl metamorphosis possibly by serving to release the thyroid hormone. This experiment should be tried on the Mexican strain of axolotl which apparently rarely spontaneously metamorphoses and hence can be safely controlled.

#### THYROIDECTOMY AND METAMORPHOSIS

Eight axolotls varying from seven to fourteen inches were thyroidectomized and at the present writing, September 1, are still larvae and show no indications of transforming. Out of the original one hundred and nine animals received from New Mexico these eight are the only ones that have not metamorphosed. It is a fairly safe assumption that these axolotls will remain permanently as larva now that the thyroid gland is lacking.<sup>1</sup>

The thyroids of several animals were removed after the onset of metamorphosis, *i.e.*, after the tail fin and gills were undergoing reduction, but in all cases the removal of the thyroid failed to prevent the completion of metamorphosis.

#### DISCUSSION

The conclusion to be drawn from these experiments is that the New Mexican strain of axolotl is entirely too unstable to work with on any problem involving the methods of feeding, injection or transplantation, where the results require a lapse of several weeks to obtain. The animals can not be controlled when the thyroid apparatus is left intact. It is evident that conclusive experiments of the above kinds on the New Mexican strain of axolotl (where the animals themselves are used as

<sup>1</sup> The thyroidectomized animals were kept for five months and then injected with iodotyrosine and iodoserumglobulin. Metamorphosis resulted within a period of twenty days following injections of either substance. Two partially thyroidectomized animals which had failed to transform were metamorphosed by injection of iodoserumglobulin. Injections of tyrosin, dibromtyrosin and globulin had no effect upon metamorphosis. Uhlenhuth's conclusion that only thyroid iodine (iodine which has undergone transformation within the thyroid gland) is effective in metamorphosing urodele larvae is invalid.

experimental material) can only be obtained by using thyroidectomized animals.

Professor Henry Laurens, of the Department of Physiology, informs me that several years ago he had a similar experience with axolotls from New Mexico. He received a shipment of several dozen in the spring, but was unable to prevent them from transforming shortly after arrival in New Haven. Only one animal of the lot failed to metamorphose and was kept two years in the laboratory, attaining a length of 14.25 inches. This individual was used by the writer for thyroid transplantation work.

The marked tendency of the New Mexican and other American axolotls to metamorphose spontaneously when moved from one locality to another prevents their being used for aquarium purposes. It is an odd fact that practically the only axolotls used as aquarium material in the United States are those that have been shipped from Europe.

The European strain seems to differ from the New Mexican form in regard to spontaneous metamorphosis, because these animals are handled by practically all aquarium dealers in Germany and can be obtained for a few cents apiece. Apparently they rarely spontaneously transform according to Jensen ('20), who has worked extensively with this strain. The curious thing about the New Mexican strain is that in their native habitat they too may remain for considerable periods as larva, yet when shipped from New Mexico to New Haven promptly metamorphose regardless of size or age. One large animal of this strain obtained by Professor Laurens failed to transform and was kept in the laboratory for two years; at the end of this time it showed no indications of metamorphosis and was killed for thyroid transplantation work.

According to Gadow ('08) the strain of axolotls established in Europe came originally from the vicinity of Mexico City. The first axolotls were brought to France by Marshal Forey in 1863, and the present strain is de-

scended from these animals. Gadow also states that the axolotls of Lake Xochimilco have never been known to metamorphose in their native habitat. However, several of the descendants of the animals taken to Europe did metamorphose, so that spontaneous transformation in the Mexican strain does sometimes occur, though rarely.

In an earlier paper ('22) the writer showed that the thyroid mechanism of axolotls is filled with physiologically active hormone capable of inducing metamorphosis but that the secretion is apparently not liberated into the blood stream, hence the retention of the larval characters despite the possession of a large well-formed gland. The thyroid of a fourteen-inch axolotl several years of age was extirpated and cut into small pieces, each piece then transplanted into an immature Anuran larva. The single axolotl thyroid promptly metamorphosed five such tadpoles within fourteen days, whereas left intact within the axolotl's body it was quite incapable of inducing transformation.

This same experiment was repeated upon thyroidectomized and hypophysectomized *Rana sylvatica* tadpoles with similar results. Small pieces of axolotl thyroid when engrafted into thyroidless and pituitaryless larvæ promptly induce metamorphosis within ten or twelve days.

It is quite clear from these experiments that axolotl neoteny is due to retention of the thyroid hormone within the gland vesicles. Under normal conditions and in its native habitat, the releasing mechanism apparently fails to act, but when the animals are shipped from one place to another and subjected to new environmental conditions metamorphosis promptly ensues. In the New Mexican strain slight stimulation is sufficient to initiate metamorphosis, but in the European and Mexican forms very powerful stimulation is needed to overcome the thyroid inhibition and release the secretion. In the European strain the following agents have been used successfully for inducing metamorphosis: thyroid feeding (Laufber-

ger '13), salicylic acid injections (Kaufman '18), iodine and iodoform injections (Hrischler '18-'19), organic iodine feeding—iodothyrosine, also injections of iodocasein, iodoserumglobulin and iodoserumalbumin (Jensen '21); and of course Marie von Chauvin's experiments are well known.

It is evident that the peculiar thyroid inhibition causing neoteny in axolotl is due to genetic factors and that the condition is hereditarily transmitted. It is interesting to note that in axolotl we have one of the best examples of hereditary transmission of an endocrine defect known. Attempts to explain neoteny by assuming that environmental agencies such as cold, altitude and the like are the chief causative factors are too crude to be seriously considered and for this reason—the aquarium dealers of Europe breed their animals as larvæ and the young grow up as axolotls, the matter of cold or altitude not entering into the question. As was previously mentioned, the European strain arose from a few animals taken to France in 1863.

Then, too, both Professor Laurens and myself received our animals from Albuquerque, New Mexico, where they breed. The animals were old when captured. The temperature of the pools in the vicinity of the city can not be very low even in winter—not nearly so cold as those of the middle western states, northern New York, Ohio, or Wisconsin—and axolotls have never been reported as occurring in these states so far as the writer is aware.

The *Ambystoma tigrinum* resulting from the metamorphosis of the axolotls during my experiments were placed in certain pools in the vicinity of New Haven where other species of *Ambystoma* are known to breed. The animals are full grown and should breed next spring (1923). By following the life history of the larvæ it is hoped that some new light may be shed upon the obscure and much debated problem of the relation of neoteny to environment.

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## SHORTER ARTICLES AND DISCUSSION

### MORE EYELESS CLADOCERA

JUST before a note appeared in *Science* (Vol. 53, pp. 462-463, May 13, 1921) concerning an eyeless cladoceran individual (a *Simocephalus exspinosis*), two additional eyeless daphnids occurred in another species of the experimental stock at the Station for Experimental Evolution. These were among offspring of some *Moina rectirostris* which were being subjected to crowding in a sex-control experiment (10 mothers in each 130 c.c. wide-mouthed bottle containing about 75 c.c. of culture medium). While these two eyeless young were released on successive days and possibly in separate bottles, they were in bottles which belonged to the same series and received the same treatment.

The precise identity of the mother of neither eyeless young could be determined (since there were 10 mothers producing parthenogenetic young in each bottle), but it is certain that the mothers were normal-eyed and were sisters, or came from mothers which were sisters. All of the mothers' collaterals, which were examined, approximately 250, had normal eyes. 302 other young, produced by the 10 mothers in the bottle in which the second of these eyeless appeared, were normal. In all about 5,953 young were microscopically examined—a few of which were presumably sisters of the eyeless individuals and the others of which were young from sisters of the mothers of the eyeless individuals. All were normal-eyed.

One of these eyeless individuals produced 5 broods, containing in all 66 young, all normals. The other produced 4 broods, containing 38 individuals, all normals. 841 offspring of daughters of the one eyeless, and 412 offspring of daughters of the other eyeless were found to have normal eyes. All examined among the collaterals of the eyeless individuals, 5,953 in all, and 1,357 direct first and second generation descendants of the eyeless mothers themselves—a total of 7,310—were normal. Hence despite the fact that there were two eyeless individuals produced by sisters (or by individuals whose mothers were sisters), while among many thousands of Cladocera previously seen under the microscope only a single similar individual had

been found, eyelessness in these individuals was clearly *not* inherited. The lack of inheritance in these *Moina rectirostris* would have been anticipated if due regard had earlier been given to a peculiar feature of the head of these eyeless individuals. This will be discussed in a later paragraph.

The next occurrence of eyeless Cladocera was in February, 1922, when seven eyeless *Moina macrocoda* were found among 147 young of the third brood from 10 mothers in a crowded bottle. The culture water in this bottle seemed rather cloudy, an appearance known frequently to be associated with unfavorable conditions which sometimes result in death to part or all of the Cladocera in such a bottle.<sup>1</sup> In the present case in addition to one eyeless male and 6 eyeless females among the 67 females and 80 males in the bottle, there were other abnormals—6 or 8 with abnormal eyes (pigment reduced or eye not completely formed) and perhaps an equal number with abnormal antennæ (certain segments missing, aborted or fused with others) and one male with an abnormal eye and an abnormal antennule. Some of the eyeless individuals and some with abnormal eyes had abnormal antennæ also. Others showed abnormality in only one feature. Since these abnormals appeared in a crowded bottle (10 mothers) it is impossible to know, but they probably did not come from a single mother. Among the next brood of young from the same mothers were a few with abnormal antennæ and slightly abnormal eyes. Subsequent young were normal.

Early attention to an interesting feature of the heads of these eyeless individuals removed any temptation to anticipate inheritance of eyelessness in these cases; and, as expected, all the numerous young examined from these eyeless individuals (and from the other abnormals as well) were normal. Since in these cases eyelessness was not hereditary some developmental accident would seem probably responsible for its occurrence. Indeed, it seems fairly evident, in view of the occurrence of other abnormalities in the same and other similar culture bottles, that these abnormalities were related to some unfavorable fac-

<sup>1</sup> In other cases such conditions of the culture medium were associated with pigmentless eyes in some of the newly released young. However, the pigment develops to its full amount in from one to five days after the young animals are released from the mother's brood chamber. Newly released young from the formerly pigmentless-eyed individuals have normally pigmented eyes from the first.

tor or factors in the environment, although nothing definite is known as to what these factors were.

A peculiar structural feature of the heads of the young eyeless individuals suggested the possible manner in which eyelessness came about in these cases. When young, the seven eyeless *Moina macrocoda* had on the anterior head margin a small nodule or excrescence which, though not so conspicuous at later stages, yet in most cases persisted through several moults. In each of these eyeless individuals the optic ganglion was reduced or lacking, and the margin of the head was readjusted to compensate for the reduced and missing organs. Substantially the same structural conditions were found with the two eyeless *Moina rectirostris*, absence or reduction of optic ganglia, the shortening of the head margin and the occurrence of a small bit of apparently necrotic material attached to the front of the head.<sup>2</sup>

It seems possible that this apparent exudate on the heads of the eyeless individuals really represented an aborted or necrotic portion of the embryo which included the primordium of the missing parts.<sup>3</sup>

The fourth occurrence of eyeless Cladocera (the eleventh eyeless individual seen) was June 26 in a crowded bottle of *Moina macrocoda*. In addition to the lack of eye and of optic ganglion, the brain proper was reduced in size. This animal was not examined until mature and an excrescence on the head, if present in the young animal, had by that time disappeared. This individual swam in small circles, although its swimming organs appeared entirely normal. It died after producing two broods (10 females and 12 males) of normal young.

The occurrences of eyeless Cladocera have included three species, eleven individuals and four different time periods. The last three occurrences, and probably the first one, were in crowded bottles, suggesting environmental factors as causative

<sup>2</sup> That this material was intimately associated with the head structures and really a part of the animal is attested by the fact that it persisted through ecdysis, whereas any material merely adhering to the external surface of the exoskeleton would be eliminated by ecdysis.

<sup>3</sup> A somewhat similar appearance in larvae arising from centrifuged eggs of *Ambystoma punctatum* was presumably correlated with failure of development of the anterior part of the head. (Banta, A. M., and Gortner, R. A., "Accessory Appendages and Other Abnormalities Produced in Amphibian Larvae through the Action of Centrifugal Force," *Jour. Exp. Zool.*, 18: 433-446, pls. 1-3. 1915.)

agents. Those which lived to produce young gave rise exclusively to normal young, indicating that genetic changes were not responsible for the abnormal heads. However, in view of the known inheritance of eyelessness in cave arthropods and vertebrates and in *Drosophila melanogaster*, it seems of interest to examine each case of profound eye modification in crustaceans and elsewhere to gain information on the origin and inheritance of any possible mutation of this character.<sup>4</sup>

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#### CROSSING-OVER INVOLVING THREE SEX-LINKED GENES IN CHICKENS

IN the course of the last year several crosses of chickens carried out at the genetics station at Anikovo (near Moscow) have made it possible to observe crossing-over in this form. The genes "suke," "tuge" and "trage" were studied. The first, suke, retards the development of feathering in the chicks, so that at the age of 1 to 1.5 months they have very small tails. The development of the wings, too, is very slow. The genes trage and tuge together cause the well-known Plymouth Rock markings, trage causing the crossbarring, and tuge (not very visible in Plymouth Rocks, where it causes the contrasts in the markings) is the same gene as silver coloring, which was first reported by Hagedoorn in the Assendelver chickens. Later (1912) Davenport observed it in the cross of Dark Brahma  $\times$  Brown Leghorn, where, however, on account of the absence of several other genes, tuge has very little expression—only as a whitish edge on the feathers.

The genes suke, tuge and trage are all present together in the Plymouth Rocks. The Russian Orloff chickens have none of these genes, a condition which may be expressed as asuke-atuge-atrage. All these genes are sex-linked, and therefore are transmitted with complete linkage from mother to son. The cross

<sup>4</sup> Since this manuscript went to the printer two more eyeless *Moyna macrocopta* were found in a crowded bottle. These two with the last one mentioned above were the only eyeless occurring among approximately 33,000 individuals microscopically examined (in sex-control experiments) during three months. The facts, that of these three two occurred in the same bottle and that the character is not inherited, again indicate clearly enough that external, not internal, factors are responsible.

Orloff male  $\times$  Plymouth Rock female gives cocks closely resembling the true Plymouth Rock, that is, crossbarred with slow feathering development. All the hens, however, are black (since in the Plymouth Rock there is also a gene for melanism, "tifa," which is not sex-linked), and they develop feathers quickly.

$\sigma$ : asuke atuge atrage atife  $\times$   $\varphi$ : suke tuge trage tifa

$F_1$   $\sigma$ : suke tuge trage tifa  $\varphi$ : asuke atuge atrage tifa

In  $F_2$  the coupling between suke, tuge and trage becomes broken, and different new combinations are to be observed in rather large numbers. More often the forms asuke-tuge-trage are obtained, colored like Plymouth Rock, but with quick development of feathering (among these there are also cocks), and conversely suke-atuge-atrage, with slow feathering, but black (when tifa is present). In one case a suke-tuge-atrage chick appeared, with slow feathering and silvery, but not crossbarred.

In the light of the Morgan theory these facts can be explained by regarding the genes suke, tuge and trage as being in a sex chromosome which cannot give crossing-over in the heterozygous sex (female). But when the same chromosome is transmitted to the  $F_1$  male, it undergoes crossing-over with its partner, which occurs most often in the space between suke on the one side and tuge-trage on the other. Crossing-over between suke-tuge on the one side and trage on the other occurs less often, wherefore the arrangement of the genes in the  $F_1$  may be represented as follows:

suke.....tuge.....trage

However, the counts of chicks which have so far been obtained in  $F_2$  are not yet large enough to ascertain definitely the order of the genes, and therefore still less the exact distances.

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[Crossing-over between "suke" (barring) and "tuge" (silvery) has also been announced by Goodale (1917) and by Haldane (1921), in the papers listed below, which were not available to the above author.

Goodale, H. D. 1917. Crossing-over in the Sex Chromosome of the Male Fowl. *Science*, N. S., Vol. 46, p. 213.

Haldane, J. B. S. 1921. Linkage in Poultry. *Science*, N. S., Vol. 54, p. 663.

Note of Transmitter, H. J. Muller.]

A FOURTH ALLELOMORPH IN THE ALBINO SERIES  
IN MICE<sup>1</sup>

IN recording the occurrence of a new mutant gene in the house mouse, allelomorphic to color and albinism, Detlefsen ('21)<sup>2</sup> described a very dilute, wild form in which the hair showed traces of a light brownish tinge with a suggestion of sootiness, and the eyes were somewhat less heavily pigmented than in the wild type. This general form of pigment reduction is also characteristic of other color allelomorphs; for in the case of the ruby-eyed rat, the ruby-eyed guinea-pig and the chinchilla rabbit (Castle '21),<sup>3</sup> the yellow pigment is very greatly reduced or even obliterated, while the darker pigments (black or brown) are at least slightly modified. The mutant mouse, however, showed a far greater pigment reduction than either the rat, guinea-pig or rabbit mutants. Breeding tests demonstrated that this dilute mouse mutant was a color-albino allelomorph, and in this respect resembled the ruby-eyed rat and guinea pig genetically (the chinchilla rabbit had not been recorded at that time), but Dr. Detlefsen pointed out that "it is hardly safe to insist that these mutations are identical. . . . We are also unable to prove that they are different, for the genes may be identical but simply give different somatic effects, since the residual inheritance can not be the same." He also suggested that the discovery of a new dilute type of mouse (which he was seeking at that time), more like the rat or guinea pig in its somatic appearances as well as in its genetic behavior, would give us more assurance that his extreme dilute mouse mutant was not the homolog of the ruby-eyed rat or guinea pig. Unusual as it may seem, I had discovered exactly such a new dilute mutant mouse in January, 1919. By comparing it with Dr. Detlefsen's set of rodent skins and by testing it in appropriate matings, I recognized its genetic significance just before his paper appeared in print.

The discovery of this new mutant mouse enables us to say at once that the extreme dilute mutant was not the homolog of the ruby-eyed rat or guinea pig or the chinchilla rabbit, and supports Dr. Detlefsen's position in hesitating to homologize

<sup>1</sup> Paper No. 22 from the Genetics Laboratory, College of Agriculture, University of Illinois.

<sup>2</sup> Detlefsen, J. A., 1921, *AMER. NAT.*, Vol. 55, p. 469.

<sup>3</sup> Castle, W. E., 1921, *Science*, N. S., Vol. LIII, p. 387.

his mutant with these forms. Dr. Detlefsen's form is evidently lower in the scale running from color to complete albinism in very much the same way that the Himalayan form is nearer to the albino than is the chinchilla rabbit.

The new mutant was procured from a fancier who had been breeding it for some time. It resembles the ruby-eyed guinea pig, ruby-eyed rat and the ruby-eyed or chinchilla rabbit (Castle '21)<sup>4</sup> in the degree of pigment reduction in the hair, but the eyes are apparently darker than those of the rat and guinea pig. I have not had an opportunity to examine the eyes of the chinchilla rabbit. It forms one of a series of quadruple color allelomorphs in the mouse and may be designated as  $c^r$ . In a scale of dominance, the four forms probably fall into the following order: ordinary intense or wild color,  $C$ ; dilute,  $c^r$  (described in this paper); extreme dilute,  $c^d$  (described by Detlefsen ('21);<sup>5</sup> and complete albinism,  $c$ . Wild color ( $C$ ) is completely dominant to the other allelomorphs, but  $c^r$  and  $c^d$  are incompletely dominant to albinism. The cross between  $c^r$  and  $c^d$  has not yet been made, but the heterozygote ( $c^r c^d$ ) will probably be found to give an intermediate shade.

The black agouti type of the homozygous mutant ( $AABBc^r c^r$ ) possesses black pigment which is reduced to a very dark dull slate-color, while yellow is greatly reduced and appears about intermediate between white and the normal yellow of the wild type. In the non-agouti type of the homozygous mutant ( $aaBBc^r c^r$ ), which can be distinguished readily from the agouti form, the black pigment is also reduced to a very dark dull slate-color, but perhaps darker than in the agouti type.

When the black agouti type of the mutant is heterozygous for albinism ( $AABBc^r c$ ), black pigment is reduced to a brownish shade and yellow is practically reduced to white. In the non-agouti type of the heterozygous mutant ( $aaBBc^r c$ ), black is reduced to a dull brown, a little lighter than the ordinary fancier's chocolate type. The heterozygous mutants, mated interse, produce the homozygous type, the heterozygous type and albinos in the ratio of 1: 2: 1.

I have not yet identified the mutant without black pigment that is in the cinnamon or brown class.

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<sup>4</sup> *Loc. cit.*

<sup>5</sup> *Loc. cit.*

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